ELEMENTS

OF

HUMAN PHYSIOLOGY

BY

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TRANSLATED FROM THE FIFTH EDITION

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TRANSLATOR'S PREFACE.

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WHEN, now two years ago, at the solicitation of several friends, I undertook the translation of Professor Hermann's ' Elements of Physiology,' I was actuated by the conviction, shared in by nearly all teachers, that an urgent need existed for an English text-book which should represent the actual state of the science. It appeared to me, at the same time, that no text-book on Physiology existed in any European language at once so concise, comprehensive, and philosophical as the work which I now introduce to the English reader, and I therefore undertook its translation.

During the progress of my task, which a multiplicity of occupations caused to be a more protracted one than I had anticipated, my early convictions as to the excellence of the work have steadily deepened.

The very condensed style of the whole work, the immense number of facts brought together under every section, and the constant assumption on the part of the Author that the reader is possessed of varied and accurate knowledge of the sciences upon which Physiology is based, may tend to dismay the student who brings to its

study but a scanty preliminary education or a lukewarm zeal, but this is a result which cannot be avoided by any author who treats his subject in a thorough manner. The conviction is, fortunately, growing every day that a thorough knowledge of Physiology is of primary importance to the medical man, and the science is now being earnestly studied, for its own sake, by many who are not connected with the practice of medicine.

With the increased facilities which are now afforded in our laboratories and lecture-rooms of studying physiology as every experimental science should be studied, a more thorough theoretical treatment of the subject than has usually been attempted in our text-books becomes desirable and expedient, and therefore I believe that by students the present work will be received as favourably as it has been by those teachers who have long known it in its original German dress.

After much hesitation and many doubts I decided not to annotate the text, for had explanatory notes, of the nature of commentaries with illustrations, been added to it, as I once intended, its appearance would have been still longer delayed, and the work would have been materially altered in character—it would have ceased to be Hermann's Physiology.

It will be obvious to the critical reader that in the execution of such a work a great responsibility rests with the translator, who in dealing with some subjects which have never been fully treated of in his own language is necessarily compelled to introduce new expressions, which thenceforward will probably find a place in the scientific nomenclature of the language.

It would occupy too much space to enter into the

philological or scientific grounds for the English equivalents which I have employed in the translation of certain little-used or even new words which occur in the German text, or of common words which acquire a special meaning from the context; to a few of these I shall, however, refer.

'Auslösende Kraft,' the term employed by Professor Hermann to express a force which removes any hindrance or impediment to the conversion of potential into kinetic energy, has been translated 'liberating-force,' and consistently 'Auslösung' has been rendered by the word 'liberation.' My friend Professor Burdon Sanderson, F.R.S., strongly advised me, though after the first sheets of the work had passed through the press, to adopt the term 'discharging-force' as the equivalent of the German expression, and chiefly for the reason that the term 'discharging' is used in English in an analogous sense, in many cases where a conversion of potential into kinetic energy is effected, as when we speak of the discharge of a gun, the discharge of a Leyden jar, &c.

'Vorstellung' has been generally rendered by the English equivalent 'consciousness,' or 'states of consciousness.' 'Seele' has been translated by 'mind.'

The word 'Leistung' has received several different meanings according to the context, being rendered by 'function,' 'act,' 'activity,' or 'energy.' This latter meaning has actually been applied to the title of Part II. of the work, where 'Die Leistungen des Organismus' has been paraphrased, 'The *Activities* or *Energies* of the Body.' I feel confident that the scientific reader will acknowledge this to be the most intelligent equivalent for the title of that division of the work which deals with those processes

in which potential is converted into kinetic energy, and in which their conversion is the most prominent phenomenon.

In the exposition of Fechner's psycho-physical law I have adopted as the equivalent of the German 'Schwellenwerth,' the term 'liminal intensity,' which was suggested to me by Dr. Sanderson, and which appeared to me a more literal and more happy rendering than 'initial intensity,' which I had adopted.

In the sections on voice and on hearing the nomenclature used is that adopted by Mr. Ellis in his translation of Professor Helmholtz's work, 'On the Sensations of Tone.'

In the accomplishment of my task I have been greatly aided by several friends, some of whom have contributed translations of portions of the book, whilst others have given me the benefit of their advice. I have, in the first place, to express my obligations to my friend and pupil, Mr. John Priestley, Platt Physiological Scholar in Owens College, for very great help in the actual translation and revision of many important sections. I have to make the same acknowledgment to my friend Dr. Julius Dreschfeld, Lecturer on Pathology in Owens College, and to Professor Burdon Sanderson, F.R.S., the latter of whom has contributed the whole of the physiological division of the section on the Organ of Hearing, in Chapter X.

To Mr. Liebreich I am indebted for having revised that section of the physiology of Vision which deals with the Horopter. Lastly, I have to thank my friend Dr. Klein, F.R.S., for having made several important suggestions in the translations of the sections on Development, in Chapter XII.

Although I have endeavoured to perform my task as

carefully as lay in my power, I am aware that numerous errors must of necessity be found in the translation of a work which deals in so technical a manner with the details of many sciences, and which in a short compass embraces many facts and quotes many authorities. For these errors I have to crave the indulgence of the reader.

ARTHUR GAMGEE.

The Owens College, Manchester:
October, 1875.

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INTRODUCTION.

PHYSIOLOGY is the science which treats of the normal processes which have their seat in the living bodies or organisms of plants and animals. The processes which are characteristic of living beings, and whose sum constitutes life, may be classified as orderly changes of (1) their chemical constituents; (2) the forces which work within them; and (3) their form. Formerly an attempt was made to explain the peculiar processes which have their seat in the animal organism, by supposing it to be endowed with properties special to it, and heritable, depending on a supposed ' *vital force.*' This vague conception has, however, been abandoned since the laws of inorganic nature have been discovered to preside over the most thoroughly investigated processes of life, and especially since the application to the organic world of a great principle of modern science has taught us the relations which exist between the changes in the matter and the forces of organised beings. Relying upon this knowledge, we believe that the forces of living are the same as those of inanimate bodies, and that they obey the same laws, and, consequently, that it will ultimately be possible to explain the hitherto incomprehensible phenomena of living beings, particularly their morphological processes, by physical and chemical laws. This conception possesses, quite apart from its probability, the great merit of introducing into the study of organic nature more precise views and more accurate research, and, although it has not been rigidly proved, will, in the present work, tacitly underlie the exposition of the processes of the human organism.

The human body, like that of every other animal, is an organism in which, by the chemical changes of its constituent parts, *potential* is converted into *kinetic* energy.

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These chemical changes depend on the presence, within the organism, of energy-yielding substances.

The greater number of the chemical operations which occur in the living body, and which are accompanied with the manifestation of kinetic energy, are oxidations, or decompositions which depend on oxidation; nevertheless, there are, in all probability, other processes which are so accompanied. The energy-yielding material of the organism is chiefly represented, on the one hand, by oxidizable (organic) combinations ; on the other by free oxygen.

The following is an instance of a simple oxidation :

$$2\ C_5H_4N_4O_2 \quad + \quad O_2 \quad = \quad 2\ C_5H_4N_4O_3$$
$$\text{Xanthine} \qquad\qquad \text{Oxygen} \qquad\qquad \text{Uric acid}$$
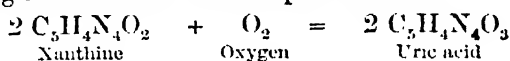
An example of a decomposition depending on oxidation is :

$$C_4H_8O_2 \quad + \quad 3\ O_2 \quad = \quad C_2H_4O_2 \quad + \quad 2\ CO_2 \quad + \quad 2\ H_2O$$
$$\text{Butyric acid} \quad \text{Oxygen} \qquad \text{Acetic acid} \qquad \text{Carbonic acid} \qquad \text{Water}$$
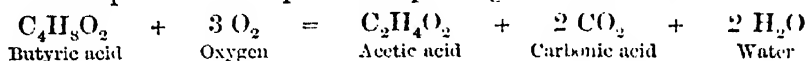
The following may be adduced as examples of other decompositions occurring in the body, and which are associated with a manifestation of kinetic energy :

a. Simple decompositions, *e.g.*

$$(1) \qquad\qquad C_6H_{12}O_6 \quad = \quad 2\ C_3H_6O_3$$
$$\text{Sugar} \qquad\qquad \text{Lactic acid}$$

$$(2) \qquad\qquad C_6H_{12}O_6 \quad = \quad 2\ C_2H_6O \quad + \quad 2\ CO_2$$
$$\text{Sugar} \qquad\qquad \text{Alcohol} \qquad \text{Carbonic acid}$$
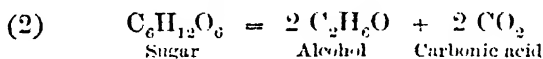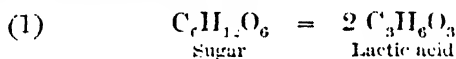
b. Hydrolytic decompositions, in which a body splits up after combining with the elements of water :

$$C_{57}H_{110}O_6 + 3\ H_2O = 3\ C_{18}H_{36}O_2 + C_3H_8O_3$$
$$\text{Stearin} \qquad \text{Water} \qquad \text{Stearic acid} \qquad \text{Glycerin}$$
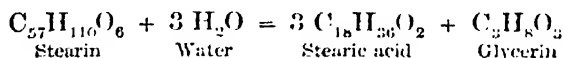
Every act of the organism must diminish, to a corresponding extent, the energy-yielding store which it contains. As the products of the chemical changes, even when they, in the first place, have definite purposes to fulfil in the body, are ultimately thrown off from it ; and, moreover, as the reconversion of these products into the substances from which they were originally derived would require the expenditure of as much energy as is generated during the process of decomposition, it follows that a restitution of energy-yielding substances can only take place from without. It is, therefore, essential, in order that the organism should continue to exist, that it be continuously supplied with free oxygen and oxidizable substances. The latter are called *the organic constituents of food.*

In addition to its energy-yielding constituents, the organism possesses other (inorganic) substances, which do not furnish it with energy. Their uses are only imperfectly ascertained, though they appear, in great part, to be mechanical. Some serve as solvents for organic bodies, some play an important part in the formation of the solid parts of the body, whilst others are in complex combination with essential organic constituents. Even the inorganic substances are continually being thrown out of the body in certain quantities, serving, in part, as solvents for the products of decomposition which have to be eliminated. The inorganic substances of the body, therefore, like the organic, have to be continually replaced by others taken from without, which constitute *the inorganic constituents of food*.

It follows from what has been said that the existence of the organism is associated with a continual movement of matter into and out of it, which constitutes what may be termed the *circulation of the matter*, or the *material exchanges* of the organism (Stoffwechsel des Organismus).

The plant takes the products of the chemical operations of the animal body (carbonic acid, water, ammoniacal salts) and reduces them; it arranges their radicals (carbon, hydrogen, nitrogen, &c.) side by side, combines them with oxygen, and, storing them up within itself as organic compounds, it restores the greater part of the liberated oxygen to the atmosphere. In the separation of the once combined molecules, a certain amount of kinetic energy is expended, which is exactly equal to the amount of potential energy remaining in the separated elements; we may, therefore, say that in the process of reduction kinetic is converted into potential energy. The kinetic energy which the plant receives is apparently yielded to it, first by conducted heat (plants cool the bodies in their vicinity), secondly by radiated heat, thirdly by absorbed light (chemical rays). The potential energy into which these forms of kinetic energy are converted is associated with the liberated oxygen and the oxidizable organic compounds stored up in the plant. (We must not forget, however, that even in plants there occur processes which are similar in nature to those which are characteristic of the animal body; thus many of the parts of plants generate heat. Further, the processes of development in the plant, as in the animal, require kinetic energy.) From what has been stated there follows the most weighty conclusion, viz. that the vegetable and animal kingdoms are mutually dependent on one another. The plant, acting as a reducing agent, converts kinetic into potential energy; the animal, acting as an oxidizing agent, converts potential into kinetic energy. The plant uses the oxidation-products of the animal, CO_2, H_2O, &c.; the animal uses the reduction products of the plant—O, on the one hand, and the organic compounds of C, H, N, O, &c., on the other. These

organic compounds built up by the plant, if we except inorganic matters, constitute the only nourishment of animals, for even carnivorous animals merely consume the elements of vegetable food which have been modified and stored up for a time in the tissues of the creatures upon which they feed.

The amount of kinetic energy developed in the chemical processes of the organism is entirely determined (in any case) by the nature of the process and the amount of the constituents which take part in it. The *modes of motion*, however, in which the kinetic energy manifests itself, the *activities* of the body, which result from the chemical changes, depend upon conditions with which we are unacquainted. We merely know that certain results are associated with specific apparatuses of the body, which we term *organs*, and which are distinguished from one another, not only by the substances which they contain (their chemical composition), but also by their peculiar structure. The most general forms of motion which result from chemical changes are heat, and changes in the state of aggregation and in form. These changes may either proceed with imperceptible slowness in the smallest parts, and are then designated *growth, division*, &c., or they manifest themselves on a larger scale as the visible motion of masses (*mechanical work*). Electricity is also one of the forms of energy which result from chemical changes; in many animals there is also an evolution of light.

The same organ can, either simultaneously or at different times, give rise to different manifestations of energy.

There exist well-known (equivalent) quantitative relations between the various forms of motion. A decomposition which, if leading to the formation of heat, develops one heat-unit, will, if it accomplishes mechanical work, perform 424 grammetres of work; one unit of heat can therefore be converted into 424 grammetres of work, and conversely.

The chemical changes, and consequently the activities of the body, are, in great part, if not altogether, subjected to a certain regulating influence, which proceeds from a peculiar apparatus which we denominate the *nervous system*. This influence, naturally, affects not only the amount and nature of the products of chemical change, but also the amount of energy which becomes kinetic, *i.e.* it affects the acts performed by the body. According to our views of the functions of an organ do we place this or that effect of the influence in the foreground. Thus in the case of a muscle we regard the influence of a nerve on its

motion, and therefore on the work which it can accomplish, as the essential effect; whilst we habitually overlook the simultaneous influence which it exerts on the quantity of the chemical products which are generated in the muscle. In glands, on the contrary, the influence of the nerves supplying them on their chemical products, viz. on the specific constituents of their secretions, appears to be the essential result, whilst the contemporaneous influence on the production of heat, *i.e.* on the evolution of kinetic energy, is usually neglected.

The mode in which this influence of the nervous system is exerted is as yet quite unknown to us. From a mechanical point of view, this influence may be regarded as a *liberating force*, i.e. as a force which leads to a conversion of a certain amount of potential into kinetic energy.

It is well known that an infinitely small liberating force may liberate large quantities of kinetic energy, and it is exceedingly probable that even the liberating forces of the nervous system, if measured as forces, would be very small in amount, and consequently that the chemical changes necessary to their evolution, as to that of all the other forces of the organism, are but of small magnitude.

A second, even more obscure, influence of the nervous system is that which relates to the kind of bodily acts by which the liberated energy manifests itself; this qualitative influence of the nervous system appears to be closely associated with its influence on the quantity of the energy transformed.

The following remarks may render more easy the conception of a 'liberating force.' A liberating force is one which removes any hindrance or impediment to the conversion of potential into kinetic energy. A clock wound up, but prevented from going by a catch, represents a certain amount of potential energy; the position of its weights or of its spring cannot then be converted into motion. So soon, however, as the catch is withdrawn, the potential energy becomes kinetic, the weight falls or the spring approaches its original form, and the clock goes. The force which removes the catch, which therefore liberates the clock, and liberates its potential energy, may be called 'the liberating force.' Its magnitude often bears no proportion to that of the energy set free; the same force which withdraws the catch which impeded the motion of a clock driven by a gramme weight, might also liberate a clock driven by a hundred weight.

Other examples of such liberations are :—

A spark which inflames a mass of gunpowder, and consequently sets free enormous quantities of energy, or a slight movement which closes the circuit of a powerful battery. There occur, however, cases of liberation in which

the liberating force does not, as in the cases cited above, instantly set free the whole store of energy, but only a portion, which bears a definite, though it may be a complicated, relation to its own magnitude. Let us take the case of a head of water confined by a sluice with a rectangular door. The quantity of water which will flow out, and the kinetic energy represented by its fall, will depend upon the height to which the sluice-door has been raised, and upon the force—here acting as a liberating force—expended in raising it.

All the phenomena of liberation which occur in the body appear to bear some resemblance to the last case which has been cited.

A closer survey of the nervous system reveals the fact that not only does it exert a liberating influence on the *organs of work* of the body, but that its own constituent parts exert a similar action one upon the other. By organs of work we may shortly designate those organs, such as muscles and glands, in which considerable amounts of energy become kinetic and apparent to us in the form of mechanical work, heat, &c.

A portion of the nervous system—that engaged in conducting—may be looked upon as consisting of series of elementary parts, of which each one possesses a certain amount of potential energy, and which are so closely connected together that the energy which has been liberated in one part serves to liberate the energy of the adjoining elementary parts; thus, a liberating force which acts on the first of these elementary parts produces a series of liberations, until at last the energy set free in the ultimate particles situated in some other organ (as an organ of work) brings about the liberation of forces within that organ. We distinguish two kinds of *liberating-chains*, possessing distinct origins and terminations. The one kind proceeds from the so-called organs of the senses, *i.e.* from organs on which an external influence (as pressure, heat, sound, light, &c.) acts as a liberating-agent, and terminates in the so-called *central organs of the nervous system*; to which we give the name of centripetal chains, or centripetal nerves. The second kind (the centrifugal chains), on the other hand, proceeds *from* the central organs of the nervous system, and terminates *in* the organs of work.

The central organs of the nervous system may, consequently, be looked upon as the points of departure and of entrance of liberating-chains. We are, however, unacquainted with the nature of the processes which, in the case of centrifugal chains,

act as liberating causes, or in the case of centripetal chains are the result of the influences which travel to the centre. In reference to these questions, we merely possess hypotheses which will be discussed in the section which treats of the central organs of the nervous system. Here, it may however be merely mentioned, that there are many cases in which the question appears to be easily solved, viz. cases in which a centripetal chain, acting through a central organ, immediately liberates a centrifugal chain, so that essentially there exists only a single chain commencing in a sense-organ and terminating in a work-organ (reflex action).

Finally, we must mention that in a part of the central organs certain material processes—amongst others such as are capable of liberating centrifugal chains and such as are the results of centripetal liberations—are accompanied, in an inexplicable manner, with wholly undefinable phenomena, which characterize what we term *consciousness.* The term *mind* may be applied to the combination of all the actual and possible states of consciousness of the organism.

It is the province of Physiology to investigate the molecular processes of the organism, and to connect with these all its functions. The means of treating in a scientific manner the phenomena of mind are completely wanting, inasmuch as these phenomena cannot be brought into relation with any of our scientific conceptions. Physiology must here, therefore, provisionally limit herself to the investigation of the organs with which they are connected. Even of the remaining tasks of the science, whose solution we may venture to designate as possible, but a few have been really accomplished.

It is difficult to follow a strictly logical course in the exposition of the facts which have been already discovered. Seeing that our knowledge of the relation between the chemical processes and the forces of the organism is so limited that it is nearly all included under the general observations which have already been made, it would be in vain to attempt to expound them in their natural and close mutual relations. It is more

convenient, therefore, to consider in two distinct parts of this work the *Material exchanges* and the *Transformations of Energy* of the organism. But here a fresh difficulty arises out of the mutual relations of the organic processes. The forces of the organism are often employed in directing its matter, so that a knowledge of these forces is requisite, in the first place, for the proper understanding of the material circulation. Hence it happens that even in the first part of this book, which treats of the Exchanges of Matter, reference is often made to movements, therefore to potential energy which has become kinetic, though, naturally, no reference is made to its origin. Conversely, our knowledge of the characteristic changes in the matter of some organs of work is so limited, that, for many reasons, it is more convenient to state what has been discovered concerning it in the second part, when treating of the *Organs of Work* (*e.g.* the muscles).

The Third Part of this book treats of the Physiology of the *Liberating Organs—i.e.* of the Nervous System. The Fourth Part discusses the origin, development, the periodic changes, and the death of the organism.

PART I.

THE EXCHANGES OF THE MATTER OF THE ORGANISM.

INTRODUCTION—CHEMICAL CONSTITUENTS OF THE HUMAN BODY.

Elements.

THE following elements enter into the composition of the human body: oxygen, hydrogen, carbon, nitrogen, sulphur, phosphorus, chlorine, fluorine, silicon;—potasssium, sodium, calcium, magnesium, iron, manganese.

Copper and lead are found as occasional and, very probably, unimportant constituents. (The supposed discovery of the former metal has probably been owing to the use of reagents containing copper, Lossen). Probably other universally diffused metals, as lithium, are present, in minute quantities, in the body.

Only a few of the above-mentioned elements occur in a free condition[1] in the body, namely:

1. Oxygen O_2 o=o, enters the body in a free state, and serves to oxidize (or burn) the substances which enter into its composition. For reasons which will be subsequently given, some surmise that it is in its condition of ozone, O_3 —o—o—o— or $\triangle$, that oxygen is able to effect these oxidations without the aid of a high temperature. Oxygen is found in all the fluids of the body, either in a state of simple solution, or loosely combined.

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[1] It must be remembered that even elements in a so-called free condition are combinations of several atoms, *e.g.* Oxygen, O_2; Ozone, O_3; Nitrogen, N_2.

The existence of a third modification of oxygen, 'antozone,' concerning whose properties statements differ, is now denied, and the phenomena ascribed to it are explained by the presence of hydric peroxide.

2. Nitrogen N_2 $N\!\!\equiv\!\!N$ is absorbed from the atmosphere in a free condition, and is consequently found dissolved in the fluids of the body. In addition, it is probably set free in the oxidation of nitrogenous organic compounds, and eliminated in this condition.

Even Hydrogen, H_2, occurs in the alimentary canal as a product of decomposition; probably it originates in the butyric acid fermentation.

Chemical Compounds.

The formation of chemical compounds from their elements or from more simple compounds, by so-called synthetic processes, has hitherto only been discovered to occur in the body to a very slight extent. The more accurately known chemical processes of the body consist, on the contrary, chiefly in the falling to pieces of complicated compounds, whose *composition* is only partially known, and whose *constitution* is entirely unknown to us; these bodies contain carbon, hydrogen, and oxygen; many contain, in addition, nitrogen; some also sulphur, phosphorus, and iron. The most important agent in bringing about this falling to pieces is the oxygen which enters the body in respiration, under whose influence complicated split up into more simple bodies, which contain more oxygen, and which are called oxidation-products. The simplest products which arise in this way are carbonic acid, sulphuric acid, phosphoric acid, and water; when these substances are formed, the individual elements combine with as much oxygen as they can in general take up. Nitrogen never separates in combination with oxygen, but it either isolates itself entirely and is then excreted in a gaseous form—an occurrence which has not been absolutely proved—or it leaves the body in simple combinations, *e.g.* as ammonia, or as ammoniacal compounds (ammonias whose hydrogen is replaced by other atomic combinations) like urea.

Between these simple combinations which the organism throws off, and the complex bodies which it receives, there exist a very large number of intermediate substances, which form the principal constituents of the body.

The most thoroughly known of these substances are those whose chemical constitution is most simple; in other words, which are soonest to be eliminated. In the latter we can with tolerable accuracy follow the course of the oxidation and the gradual simplification of the combinations; many of these compounds can be obtained by the oxidation of the substances which precede them, and conversely many of the more simple compounds can be synthetically obtained from their elements. The origin of the more complicated and little known compounds cannot, however, with equal certainty, be referred to oxidation, and it is possible (nay, to a certain extent, probable) that in their production synthetic processes come into play.

A number of substances which enter the body do not undergo such changes as have been alluded to, but pass through it without any change taking place in the grouping of the atoms which compose them. These so-called inorganic matters play a part in the body which is not yet thoroughly known. The chief of these, *water*, serves in the body as the general solvent : it forms, in so far as regards bulk, the chief constituent of all the organs but the bones, and it is received into, and separated from, the body in large quantities, a small quantity being formed in the body.

The other inorganic matters are the so-called inorganic salts. They also occur in all parts of the body, but (except in the bones, which are composed mainly of salts) only in small quantity; when the tissues of the body are burned these salts remain as ' ashes.' Their importance in the organism is only imperfectly understood. In great part they appear to be not merely simply dissolved, but to exist in the form of unknown chemical compounds with the more complex (organic) constituents of the body. We can only thus explain the constant relation which they bear to other substances (*e.g.* in the bones) and the fact that the solubility and behaviour of certain bodies (*e.g.* the albuminous bodies) depend very much upon the salts which are present with them. Our knowledge of the salts which are really present in the organism is, moreover, still very incomplete, seeing that chemical analysis of the ashes only acquaints us with the acids and metals, but not with the salts which they contain; and, further, a portion of the acids, which

occur in the ashes, are only formed in the process of combustion (*e.g.* phosphoric, sulphuric, and carbonic acids).

Amongst the salts which are found in the excreta, there are some which have not entered the body in the food, but which originate within it. This is the case with carbonates, sulphates, and phosphates.

The following chemical compounds occur in the body :—

1. Water H_2O H—O—H, as has already been remarked, is a general solvent, and one of the chief constituents of all the juices and tissues of the body (it forms about 70 per cent. of the whole body). It is continually being taken into the body in large quantities with the food, and continually being excreted ; small quantities are formed in the body by the oxidation of the hydrogen of organic compounds.

Peroxide of Hydrogen,—HO H—O— or H_2O_2 H—O–O—H, according to some, occurs in the body and plays a part in the oxidation-processes which go on within it.

2. Acids and Salts.

The following acids exist in part free, in part in salts, in part as constituents of complex compounds to be afterwards alluded to (ethers, amido-compounds).[1]

a. *Inorganic Acids* (i.e. *containing no Carbon*).

1. Hydrochloric Acid HCl Cl—H appears to exist in a free state in the gastric juice (perhaps as a more complex acid compound). (See Chap. II.) Its salts (chlorides) are widely diffused throughout the body, *e.g.* sodium chloride, calcium chloride, &c.

2. Sulphuric acid $S''O_2(OH)_2$

$$H—O—S—O—H$$
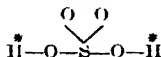
occurs in the body in salts (neutral sodium sulphate, calcium sulphate), and in more complex compounds (see Taurine, Albuminous Bodies).

The acid secretion of Dolium galea contains free sulphuric acid.

[1] In the graphic formulæ of acids which follow, those hydrogen atoms which are replaceable by metals are indicated by an appended asterisk ; according to the number of these asterisks the acid is mono-, di-, or polybasic.

3. Phosphoric acid (common, tribasic or *c*-phosphoric acid)

$$P'''O\,(OH)_3$$
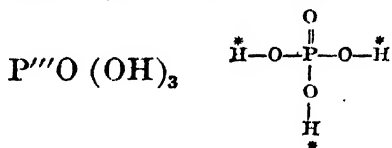
occurs in salts, as neutral and acid potassium and sodium phosphates, basic calcium phosphate, basic magnesium phosphate, phosphate of magnesium and ammonium (PO_4MgNH_4), and frequently in more complex compounds (see below Glycerin-phosphoric Acid, Lecithin).

4. Silicic acid SiO_2 $o=si=o$ has been found in some tissues of the body, perhaps only as an accidental constituent, through the inhalation of sand dust.

b. Organic Acids (i.e. containing Carbon).

5. Fatty acids (general formula $C_nH_{2n-1}O\,(OH)$.)
The series of the fatty acids at present known includes :

Formic acid	$CHO(OH)$
Acetic acid	$C_2H_3O(OH)$
Propionic acid	$C_3H_5O(OH)$
Butyric acid	$C_4H_7O(OH)$
Valerianic acid	$C_5H_{10}O_2$
Caproic acid	$C_6H_{12}O_2$
Oenanthylic acid	$C_7H_{14}O_2$
Caprylic acid	$C_8H_{16}O_2$
Pelargonic acid	$C_9H_{18}O_2$
Capric acid	$C_{10}H_{20}O_2$
Laurostearic acid	$C_{12}H_{24}O_2$
Myristic acid	$C_{14}H_{28}O_2$
Palmitic acid	$C_{16}H_{32}O_2$
Margaric acid	$C_{17}H_{34}O_2$ (probably a mixture of $C_{16}H_{32}O_2$ and $C_{18}H_{36}O_2$)
Stearic acid	$C_{18}H_{36}O_2$
Arachidic acid	$C_{20}H_{40}O_2$

These monobasic acids form a 'homologous' series ; their boiling point rises 19 C° with every addition of CH_2 ; those which contain less carbon are fluid and volatile, those which contain

more carbon are solid and not volatile. The latter are obtained from the former, by oxidation, CH_2 being removed (carbonic acid and water being formed).

$$C_4H_8O_2 + 3O = C_3H_6O_2 + CO_2 + H_2O$$
Butyric acid   Propionic acid
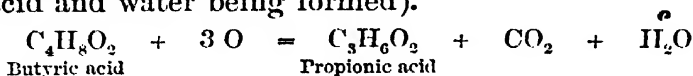
Free fatty acids are frequently found in the analysis of the constituents of the body; yet their presence during life has not been positively determined. The solid fatty acids occur sometimes in a crystallized condition within cells which previously contained fats. Alkaline salts of the fatty acids (soaps, soluble in water), further amido-compounds (see below Glycine, Leucine), and chiefly certain *ethereal* compounds of the fatty acids (see below Neutral Fats) occur in many of the constituent parts of the body. The fatty acids are in addition constituents of still more complicated compounds (see Lecithin).

6. *Glycollic Acids* (general formula $C_nH_{2n-2}O(OH)_2$).

The glycollic acids are derived from the fatty acids by oxidation, by the substitution of one H-atom by OH: even the H of the OH can be replaced by a metal, so that these acids are dibasic.

From those fatty acids which contain more than two carbon atoms (viz. from propionic acid upwards) several isomeric glycollic acids can be obtained, according to the carbon atom to which the second OH group adds itself; thus arise, for instance, the two isomeric lactic acids (oxypropionic acids), which differ in their salts.

The following are the glycollic acids as yet known:

Carbonic acid (oxyformic acid) $CO(OH)_2$

Glycollic acid (oxyacetic acid) $C_2H_2O(OH)_2$

Lactic acid (oxypropionic acid) : $C_3H_4O(OH)_2$

     Sarcolactic acid

     Ordinary lactic acid

Butylactic acid (oxybutyric acid) $C_4H_8O_3$
Valerolactic acid (oxyvalerianic acid) $C_5H_{11}O_3$
Leucic acid (oxycaproic acid) $C_6H_{12}O_3$
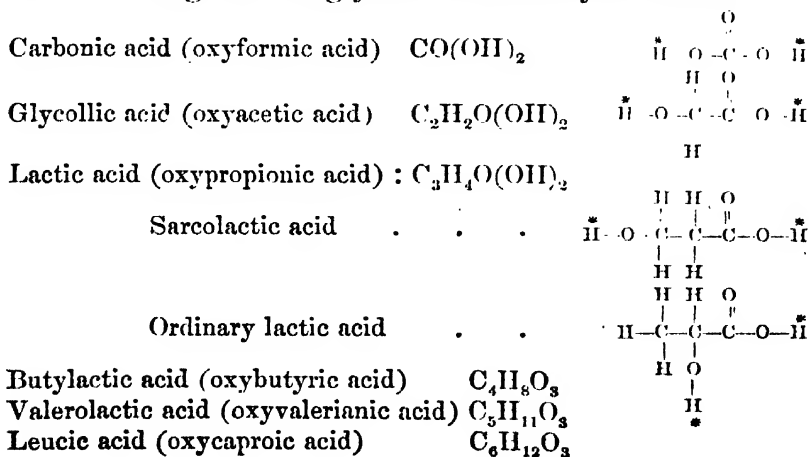
Of these acids only carbonic and the two lactic acids occur in the organism ; glycollic and leucic acids (oxyacetic and oxycaproic acids) are obtained from glycine (amido-acetic acid) and leucine (amido-caproic acid), by the action of nitrous acid (see below).

Carbonic acid.—Carbonic acid as it has been represented in the above graphic formula does not exist in a free state ; we are only acquainted with its anhydride CO_2 o=c=o.

Carbonic acid occurs either in the free state (as absorbed gas), in the form of neutral and acid salts, or in amido-compounds (as Urea), in nearly all the component parts of the body, and is excreted in all these forms in large quantities as the principal oxidation-compound of the body. The carbonates which occur in the ash, are generally, in part, produced during the process of ignition. The most important carbonates found in the body are, sodium carbonate, acid sodium carbonate (Na_2CO_3 and $NaHCO_3$), calcium carbonate ($CaCO_3$), and magnesium carbonate ($MgCO_3$).

Sarcolactic acid is an important product of the chemical changes which go on in muscle ; ordinary lactic acid is found in various fluids of the body, being probably a product of the lactic fermentation of sugar (see below.)

7. *Oxalic Acids* (general formula $C_nH_{2n-4}O_2(OH)_2$).

These are dibasic acids obtained by the oxidation of the fatty or glycollic acids (H_2O being removed). The members of the series which have to be considered here are the following :

Oxalic acid	$C_2O_2(OH)_2$	
Malonic acid	$C_3H_2O_2(OH)_2$	
Succinic acid	$C_4H_4O_2(OH)_2$	
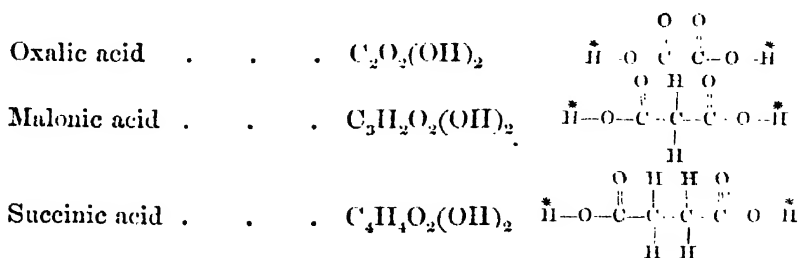
Of these, oxalic acid, and perhaps succinic acid (although this has been lately disputed), occur in the organism in the form of salts ; all three, however, occur in more complex compounds (see below Urea, Uric Acid, &c.)

8. *Oleic Acids* (general formula $C_nH_{2n-3}O(OH)$.)

These monobasic acids may be represented as fatty acids, in which two of the carbon affinities are not saturated (at least by H). Some of the members of the series are:

Acrylic acid	.	.	.	.	$C_3H_3O(OH)$
Crotonic acid	.	.	.	.	$C_4H_5O(OH)$
Angelic acid	.	.	.	.	$C_5H_7O(OH)$
Oleic acid	.	.	.	.	$C_{18}H_{33}O(OH)$

$$\underset{\text{H}}{\text{H}}-\overset{\text{H}}{\underset{|}{\text{C}}}-\overset{\text{H}}{\underset{|}{\text{C}}}-\overset{\text{O}}{\text{C}}-\text{O}-\text{H}$$

or

$$\text{H}-\overset{\text{H}}{\underset{|}{\text{C}}}-\overset{\text{H}}{\underset{|}{\text{C}}}-\overset{\text{O}}{\text{C}}-\text{O}-\text{H} \quad .$$

Of these acids only oleic acid occurs in the body, and when it does so it is in the same compounds as those of the fatty acids (as a soap, as a neutral fat (olein), or in lecithin).

9. *Cholic Acids.*

The acids belonging to this group are of yet more unknown and at any rate more complex constitution. They are insoluble in water, but form easily soluble soap-like alkaline salts, and possess a common and characteristic reaction (Pettenkofer's test). When they are heated with sugar and concentrated sulphuric acid to 60° C a purple violet colouration is produced.

They occur in the bile and in the intestinal contents of all animals, chiefly as complex compounds (conjugated bile-acids, see below *Glycine*).

Those at present known are

Cholic acid	.	.	$C_{24}H_{40}O_5$		
	Anhydrides of this acid	Choloidic acid	.	$C_{24}H_{38}O_4$
		Dyslysin	.	.	$C_{24}H_{36}O_2$
Hyocholic acid	.	.	$C_{25}H_{40}O_4$		
		Hyodyslysin	.	$C_{25}H_{38}O_3$
Chenocholic acid	.	$C_{27}H_{44}O_4$		
Guanogallic acid	.	?		
Lithofellic acid	.	$C_{20}H_{36}O_2$		

10. *Aromatic Acids.*

These are acids which are derived from the atomic group benzol C_6H_6. In this very stable group each H-atom can be replaced by a monatomic atom or group of atoms; amongst others the above-mentioned fatty acids. We may explain the relations of benzol by saying that the monatomic group phenyl C_6H_5 ($= C_6H_6 - H$) can replace one atom of hydrogen in a large number of combinations, *e.g.*
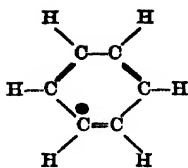
C_6H_6
Benzol
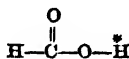
CH_2O_2
Formic acid
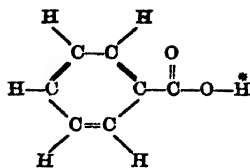
$CH(C_6H_5)O_2$
Phenyl-formic or Benzoic acid

The following are aromatic acids which possess some physiological interest:

Benzoic acid (Phenyl-formic acid) . . . $CH(C_6H_5)O_2$
Chlorobenzoic acid (Chlorophenyl-formic acid) $CH(C_6H_4Cl)O_2$
Salicylic acid (Oxyphenyl-formic acid) . . $CH(C_6H_4[OH])O_2$
Anisic acid (Methoxyphenyl-formic acid) . $CH(C_6H_4[O.CH_3])O_2$

These acids do not occur as regular constituents of the body, yet they pass through it, after having been introduced as constituents of vegetable food, and in the body form peculiar compounds (see Hippuric Acid). Possibly they also form part of more complex bodies, as of Tyrosine, which is closely related to them, and which is a product of the decomposition of the albuminous substances.

3. Alcohols.

Of undoubted alcohols only one occurs in the body, viz. Cholesterin $C_{26}H_{43}(OH)$. The constitution of this body is yet unknown; it is contained in the tissues composing the nervous system, in bile, and in the blood corpuscles.

Cholesterin is insoluble in water, easily soluble in ether and hot alcohol; it crystallizes from its solutions in the latter in the form of rhombic tables, which assume a blue colour when treated with sulphuric acid and iodine.

Glycerin, $C_3H_5(OH)_3$, is a triatomic alcohol (see graphic formula, page 19); it probably only occurs in the body in the form of ethers.

To the group of alcohols probably belong the different varieties of sugar (polyatomic alcohols), whose constitution is unknown.

The different sugars are crystalline, soluble, bodies, possessed of a sweet taste; their solutions deviate the plane of polarised light, and in consequence of the ease with which they are oxidised, they reduce many metallic oxides. They split up, under the influence of certain organisms (yeast-cells) and other so-called ferments, into simpler compounds (products of fermentation), heat being evolved during the process. The following varieties of sugar occur in the organism:

Grape sugar $C_6H_{12}O_6$ (*Synonyms*—Starch sugar, Diabetic

sugar, Liver sugar) occurs in minute quantities in the blood, in the liver, in the muscles, and in the urine (?). In diseased conditions it may occur in large quantities.

This group of atoms is besides contained in many of the more complex constituents of the body (see below). It rotates the plane of polarisation to the right.

Fermentations of sugar: *a.* Splitting up into alcohol and carbonic acid ($C_6H_{12}O_6 = 2\,C_2H_6O + 2\,CO_2$) under the influence of yeast;

b. Splitting up into lactic acid (see page 14) ($C_6H_{12}O_6 = 2\,C_3H_6O_3$), in the presence of decomposing albuminous bodies.

Sugar of Milk, $C_{12}H_{22}O_{11}$, is a constituent of milk, which rotates the plane of polarised light to the right. This sugar can *directly* only undergo the lactic acid fermentation, but when boiled with dilute sulphuric acid it is converted into a sugar (lactose) capable of undergoing the alcoholic fermentation.

Inosite, $C_6H_{12}O_6$, is a constituent of the muscles; it does not rotate the plane of polarisation; it is susceptible of the lactic acid fermentation.

The different sugars and their anhydrides are usually designated by the term 'carbohydrates,' which merely expresses that, in addition to carbon, they contain hydrogen and oxygen in the proportion in which these elements are contained in water (H_2O).

4. Ethers and Anhydrides.

When alcohol-radicals or acid-radicals, or both alcohol and acid-radicals are held together by atoms of oxygen, ethers are formed; when several similar radicals are united together in this fashion, the compounds are called anhydrides.

$$\begin{array}{ccccc}
H & H & & H & H \\
| & | & & | & | \\
H-C-C-O-C-C-H \\
| & | & & | & | \\
H & H & & H & H
\end{array}$$
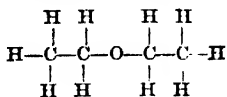
$C_2H_5.O.C_2H_5$
Diethyl ether (common
ether or alcohol anhydride)

$$\begin{array}{ccccc}
H & H & O & H \\
| & | & \| & | \\
H-C-C-O-C-H \\
| & | & & | \\
H & H & & H
\end{array}$$
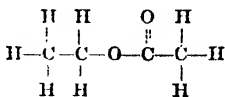
$C_2H_5.O.C_2H_3O$
Acetyl-ethyl-ether
(Acetic ether)

$$\begin{array}{ccccc}
H & O & O & H \\
| & \| & \| & | \\
H-C-C-O-C-C-H \\
| & & & | \\
H & & & H
\end{array}$$
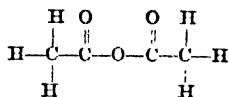
$C_2H_3O.O.C_2H_3O$
Diacetyl oxide
(Acetic anhydride)

The ethers and anhydrides are formed from alcohols and acids by a removal of H_2O, and are reconverted into them when they combine with H_2O. The first process is a synthesis, the second a process of decomposition; one may distinguish both these processes from other syntheses and decompositions, by applying to them the term of *hydrolytic*. The part which water plays in them is exhibited by the following diagram, which

shows how the action of water leads to the splitting of acetic ether into alcohol and acetic acid.

Acetic ether
Elements of water
Alcohol   Acetic acid
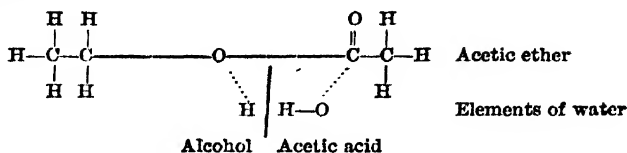
Hydrolytic decompositions sometimes occur on mere contact with water, at other times under the influence of boiling water (sometimes only at temperatures above that of boiling water, '*superheating*'), or under the influence of boiling water and mineral acids; lastly, they occur at moderate temperatures under the influence of certain ('*hydrolytic*') ferments (see p. 35). The following ethers and anhydrides occur in the body :

1. *Glyceric ethers.*—*a.* The neutral fats (see their graphic formulæ) are ethers derived from the triatomic alcohol glycerin (p. 17), the fatty acids (p. 13), and oleic acid (p. 16).

The animal fats are olein (more accurately triolein), which is fluid, in contradistinction to those which follow, which are solid, stearin, margarin (compare p. 13), and palmitin; in addition, the following are present in milk, constituting the fat of butter : myristin, caprinin, caprylin, capronin, butyrin.

The neutral fats are fluid (oils) or easily melted, insoluble in water, easily soluble in ether and hot alcohol; when fluid, they render paper translucent (grease-spots) ; when mixed with *colloid* substances and water, they admit of being broken up into fine drops, so that the fluid becomes white and opaque (emulsion). Under the influence of hydrolytic ferments, or when superheated with water (see above), they combine with the elements of water, glycerin and free fatty acids being liberated ; the latter, if volatile, are the cause of *rancid* smell.

These fats are likewise decomposed by alkalies, alkaline salts of the fatty acids (soaps) being formed, which are soluble in water; solutions of these dissolve fats.

b. To the neutral fats is also connected another, but acid, glyceric ether, viz., glycerinphosphoric acid, $C_3H_5(OH)_2 O(PO[OH])_2$, which is a combination of glycerin and phosphoric acid, minus a molecule of water.
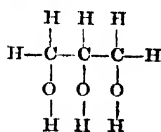
$C_3H_8O_3$
Glycerin (see page 17)
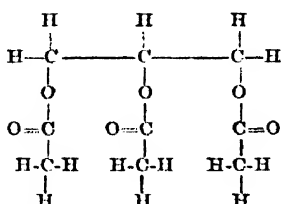
$C_3H_5.O_3(C_2H_3O)_3$
Triacetyl-glycerine ether
Triacetin (a neutral fat)
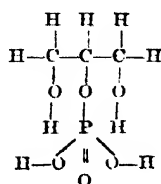
$C_3H_9PO_6$
Glycerinphosphoric acid

Glycerinphosphoric acid is a product of the decomposition of Lecithin (p. 21).

2. In spermaceti (which is obtained from the cranial cavities of certain whales) there occur some (monatomic) ethers of the fatty acids with cetyl-alcohol (ethal) $C_{16}H_{33}$.OH, viz., palmitic-cetyl-ether $C_{16}H_{33}O.C_{16}H_{31}O$.

3. *Anhydrides of Sugar.*—Certain substances are very widely diffused through the vegetable kingdom, which, when subjected to hydrolytic influences (see above: boiling with dilute acids, action of certain ferments), combine with water and form sugar, and are, therefore, to be considered the anhydrides of sugar.

The most characteristic of these substances are the following: gum $C_{12}H_{22}O_{11}$, starch $C_6H_{10}O_5$, cellulose, $C_6H_{10}O_5$, and the substance intermediate between starch and sugar, viz., dextrin, $C_6H_{10}O_5$.

The formulæ of these bodies, which appear to hold the same relation to the sugars that the ethers bear to the alcohols, are probably multiples of the above (starch being $C_{12}H_{20}O_{10}$ or $C_{18}H_{30}O_{15}$), their 'conversion' into sugar probably, in reality, being a process of decomposition. Probably milk sugar, which, under hydrolytic influences, is changed into a variety of sugar (lactose), allied to grape sugar, is an ether of lactose; cane sugar apparently behaves in the same way.

Other bodies which occur in plants, and which are termed *glucosides* are ethers built out of sugar and other atomic groups, and split· up under hydrolytic influences into these and into grape sugar.

In the animal body the only anhydride of sugar which is present is—

Glycogen $C_6H_{10}O_5$ (or a multiple of this formula). This substance is a constituent of the liver, of the muscles, and, it appears, of all embryonic organs; it is soluble in water, yielding an opalescent solution. By the red colour which is formed when it is treated with iodine, and in its power of deviating the plane of polarisation to the right, it appears to approach dextrin most closely. By the action of acids and ferments it is easily transformed into (dextrin? and) sugar.

In the brain there is also found a starch-like body, which is coloured blue by iodine.

Some glucosides occur in the body (see Protagon, Chondrin).

5. Ammonia and Ammoniacal Derivatives.

1. *Ammonia* NH_3 and its salts, the so-called salts of Ammonium, occur in traces in many of the constituents of the body, *e.g.* in the blood.

Ammonia can take part in the formation of compounds either by the monatomic group NH_2, or the diatomic group NH, replacing one or two

hydrogen atoms; in other words, the hydrogen atoms in ammonia may be replaced by monatomic or polyatomic molecules.

To the group of ammonia-derivatives belong nearly all the nitrogenous substances of the body, with whose constitution we are well acquainted. These nitrogenous bodies originate in the albuminous substances and their derivatives; in these the nitrogen is probably present in great part in the form of ammonia, although a portion of it is contained as cyanogen, seeing that some nitrogenous substances contain also cyanogen (*e.g.* uric acid). The following bodies belonging to this class must be mentioned:

a. *Amines,*

which are compounds in which the H-atoms of ammonia, or of ammonium-hydrate, are replaced by hydrocarbon groups, for example:
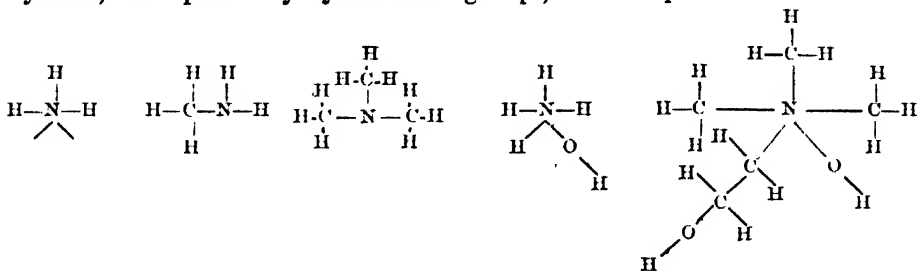
NH_3	$NH_2(CH_3)$	$N(CH_3)_3$	NH_4OH	$N(CH_3)_3(C_2H_5O)OH$
Ammonia	Methylamine	Trimethy-lamine	Ammonium-hydrate	Choline or Neurine

2. Methylamine, $NH_2(CH_3)$ and

3. Trimethylamine, $N(CH_3)_3$, occur as products of the decomposition of choline and creatine.

4. Choline or neurine, $C_5H_{15}NO_2$, trimethyl-oxyethyl-ammonium-hydrate, is one of the products of the decomposition of lecithin (see below). It is obtained synthetically from glycocol and trimethylamine, as may be easily understood by studying the graphic formula of choline; for when we unite the two groups which are joined to the nitrogen by means of the oblique lines, we obtain the graphic formula which represents glycocol, while trimethylamine remains.

As a salt of choline must be mentioned

Lecithin, $C_{44}H_{90}NPO_9$. This body is a constituent of nerve matter, of blood, of semen, of yolk of egg, &c., in which it appears to be present in complex combinations (see Protagon, Vitellin).

By boiling with baryta, lecithin yields stearic acid, glycerinphosphoric acid, and choline:

$$C_{44}H_{90}NPO_9 + 3 H_2O = 2 C_{18}H_{36}O_2 + C_3H_9PO_6 + C_5H_{15}NO_2$$

Lecithin   Stearic acid   Glycerin-phosphoric acid   Choline
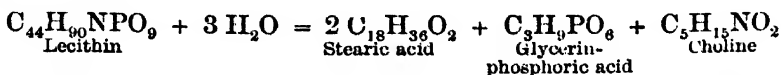
It is considered (Diaconow) as distearyl-glycerinphosphate of choline (in

the radical or residue of glycerinphosphoric acid two H-atoms are re-
placed by the radical of stearic acid). According to this view, the (abbre-
viated) formula of lecithin would be

$$
\begin{array}{c}
\text{H} \quad \text{H} \quad \text{H} \\
(C_{18}H_{35}O)-\overset{|}{C}-\overset{|}{C}-\overset{|}{C}-(C_{18}H_{35}O) \\
\text{HO} \quad \text{O} \quad \text{OH} \quad CH_3 \\
\text{HO}-P-O-N<^{CH_3}_{CH_3} \\
\overset{||}{O} \qquad C_2H_5O
\end{array}
$$
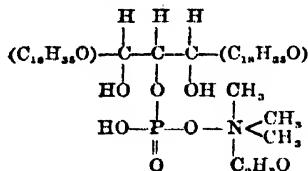
In addition to distearin-lecithin, there appears to be also a diolein-leci-
thin, an oleo-palmitin-lecithin, &c. According to another view (Strecker),
lecithin is not a choline-salt of distearyl-glycerinphosphoric acid, but it is
an ether-like body combined with the C_2H_5O molecule of choline.

5. *Guanidine, imido-carbodiamide,* $C(NH_2)_2(NH)$ (or diamido-imido-
methane) is a product of the decomposition of guanine. It is obtained syn-
thetically from chloropicrin $C(NO_2)Cl_3$ and ammonia:

$$CNO_2Cl_3 + 4\ NH_3 = C(NH_2)_2(NH) + N_2 + 2\ H_2O + 3\ HCl.$$
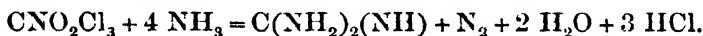
Guanidine is closely related to urea.

6. *Methyluramine,* methylated guanidine (guanidine, in which the group
CH_2 has entered, as in the groups of the homologous series of fatty acids, p.
13), or *diamido-imido-ethane,* $C_2H_2(NH_2)_2(NH)$, is a product of the de-
composition of creatine.

b. Amides,

are compounds in which the OH-group in acids is replaced by
NH_2.

7. Urea, *carbamide,* $CO(NH_2)_2$

$$
\begin{array}{ccc}
\text{O} & \text{H} \quad \text{O} & \text{H} \quad \text{O} \quad \text{H} \\
\overset{||}{H-O-C-O-H} & H-N-C-O-H & H-N-C-N-H \\
CO(OH)_2 & CO(NH_2)OH & CO(NH_2)_2 \\
\text{Carbonic acid} & \text{Monamide of carbonic acid} & \text{Diamide of carbonic acid} \\
& \text{(Carbamic acid)} & \text{(Carbamide or Urea)}
\end{array}
$$
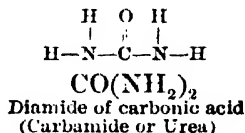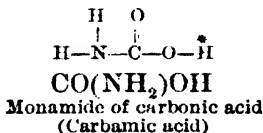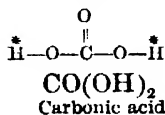
is one of the simplest amido-compounds, and is the chief pro-
duct of the oxidation of nitrogenous substances in the organism;
it is excreted in large quantities in the urine.

Urea is crystalline, easily soluble in water and alcohol, forms a sparingly
soluble salt with nitric acid, and gives a white precipitate with solution
of mercuric nitrate. In the presence of decomposing substances, when boiled
with alkalies, and when superheated with water, it combines with $2\ H_2O$,
and is converted into ammonium-carbonate: $CO(NH_2)_2 + 2\ H_2O =$
$CO(O.NH_4)_2$

$$
\begin{array}{cc}
\text{H} \quad \text{O} \quad \text{H} & \text{H} \quad \text{O} \quad \text{H} \\
H-N-C-N-H & H-N-O-C-O-N-H \\
& \text{H} \quad \text{H} \qquad \text{H} \quad \text{H} \\
CO(NH_2)_2 & CO(O.NH_4)_2 \\
\text{Urea} & \text{Ammonium carbonate}
\end{array}
$$
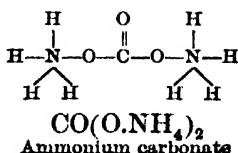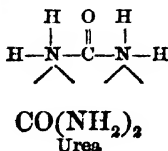
Urea was the first organic substance which was synthetically obtained (Wöhler); it can be made artificially by many processes, as by heating ammonium cyanate, · when a re-arrangement of atoms takes place $(CN(O.NH_4) = CO(NH_2)_2)$.

$$N\equiv C-O-\overset{\bullet}{H} \qquad N\equiv C-O-\overset{\overset{H\quad H}{\diagdown\diagup}}{\underset{\overset{\diagup\diagdown}{H\quad H}}{N}} \qquad \overset{\overset{H\quad O\quad H}{|\quad||\quad|}}{H-N-C-N-H}$$

$$\text{CN(OH)} \qquad\qquad \text{CN(O.NH}_4) \qquad\qquad \text{CO(NH}_2)_2$$
Cyanic acid   Ammonium cyanate   Urea
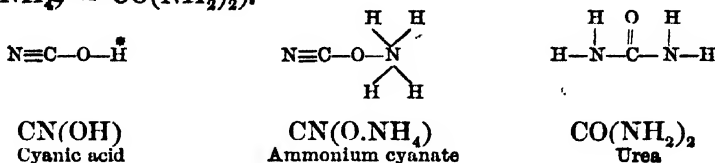
Urea can also be prepared from carbonyl chloride (phosgene gas) and ammonia:

$$COCl_2 + 2\,NH_3 = CO(NH_2)_2 + 2\,HCl$$

$$\overset{\overset{H}{|}}{H-N-H} \quad \overset{\overset{O}{||}}{Cl-C-Cl} \quad \overset{\overset{H}{|}}{H-N-H} \qquad\qquad Cl-H \quad \overset{\overset{H\ O\ H}{|\ ||\ |}}{H-N-C-N-H} \quad H-Cl$$

$$\text{NH}_3 \qquad \text{COCl}_2 \qquad \text{NH}_3 \qquad\qquad \text{HCl} \qquad \text{CO(NH}_2)_2 \qquad \text{HCl}$$
Phosgene gas.   Urea.
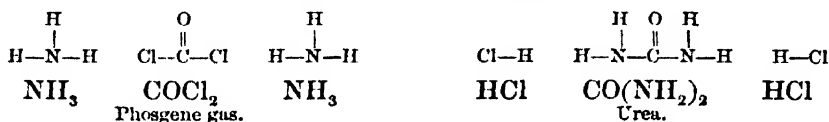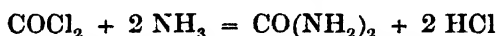
Urea differs from guanidine in that in the latter body the carbon atom is joined to the diatomic molecule NH, instead of to an O-atom.

In both the NH_2-molecules in urea, the H-atoms admit of being replaced by alcohol- or acid-radicals. Combinations of the latter kind, namely, where $2H_2$ are replaced by diatomic acid-radicals, are often obtained, in addition to ordinary urea, in the artificial oxidation of uric acid (which is itself a body of the same kind, only more complex). The radicals of the oxalic acid series and their immediate derivatives are, indeed, such compound ureas; some of them are called acids, for the last H-atom of the amide group, which is still present, can be replaced by a metal. Some of these bodies are: Parabanic acid (oxalyl-urea) $CO(NH)_2(C_2O_2)$, Barbituric acid (malonyl-urea) $CO(NH)_2(C_2H_2O_2)$, Dialuric acid (tartronyl-urea) $CO(NH)_2$ $(C_3H_2O_3)$, Alloxan (mesoxalyl-urea) $CO(NH)_2(C_3O_3)$.

Parabanic acid   Barbituric acid   Dialuric acid   Alloxan
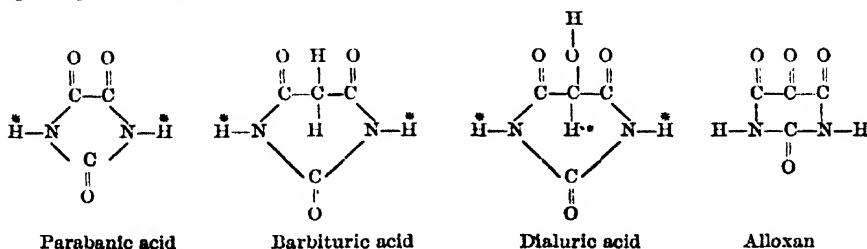
When subjected to hydrolytic processes these ureas combine with one or two molecules of H_2O; in the first case the ring, as it were, opens, and an acid is formed in which only one of the OH groups is replaced by urea; if two molecules, however, enter, urea entirely separates from the acid; e.g., in the case of parabanic acid, the first molecule of water yields oxaluric acid.

$$\overset{\overset{H\ \ O\ \ H\ \ O\ \ O}{|\ \ ||\ \ |\ \ ||\ \ ||}}{H-N-C-N-C-C-O-H}$$

$$\text{C}_3\text{H}_4\text{N}_2\text{O}_4$$
Oxaluric acid
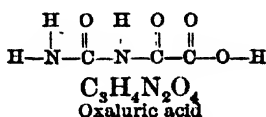
The second molecule of water leads to the formation of

$$\underset{\substack{CO(NH_2)_2 \\ \text{Urea}}}{H-\overset{\overset{\displaystyle H}{|}}{N}-\overset{\overset{\displaystyle O}{\|}}{C}-\overset{\overset{\displaystyle H}{|}}{N}-H} \quad \text{and} \quad \underset{\substack{C_2O_2(OH)_2 \\ \text{Oxalic acid}}}{H-O-\overset{\overset{\displaystyle O}{\|}}{C}-\overset{\overset{\displaystyle O}{\|}}{C}-O-H}$$
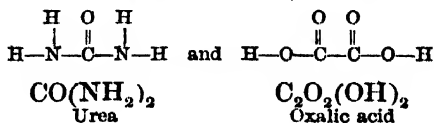
When reduced, alloxan furnishes alloxantin ($C_8H_4N_4O_7$).

$$2\,C_4H_2N_2O_4 + H_2 = C_8H_4N_4O_7 + H_2O.$$
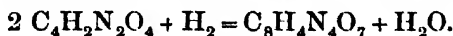
Alloxantin is an ether-like combination of alloxan and dialuric acid (see above), and on the addition of H_2O yields these two substances:

$$C_8H_4N_4O_7 + H_2O = C_4H_4N_2O_4 + C_4H_2N_2O_4$$

Dialuric acid is obtained by the further reduction of alloxan or alloxantin:

$$C_4H_2N_2O_4 + H_2 = C_4H_4N_2O_4$$
$$C_8H_4N_4O_7 + H_2O + H_2 = 2(C_4H_4N_2O_4)$$
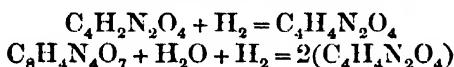
c. *Amido-Acids*

are acids in which hydrogen atoms of the acid radical are replaced by NH_2, for instance:

$$\underset{\substack{C_2H_3O(HO) \\ \text{Acetic acid}}}{H-\overset{\overset{\displaystyle H}{|}}{\underset{\underset{\displaystyle H}{|}}{C}}-\overset{\overset{\displaystyle O}{\|}}{C}-O-H} \qquad \underset{\substack{C_2H_2(NH_2)O(OH) \\ \text{Amidoacetic acid or glycocine}}}{H-\overset{\overset{\displaystyle H}{|}}{N}-\overset{\overset{\displaystyle H}{|}}{\underset{\underset{\displaystyle H}{\wedge}}{C}}-\overset{\overset{\displaystyle O}{\|}}{C}-O-H}$$
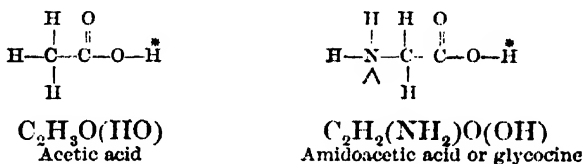
The amido-acids behave, on the one hand, as acids, on the other as bases, inasmuch as their ammoniacal residue combines with acids, *e.g.*

$$\underset{\substack{\text{Glycocine-silver compound} \\ \text{Silver Amido-Acetate}}}{H-\overset{\overset{\displaystyle H}{|}}{N}-\overset{\overset{\displaystyle H}{|}}{\underset{\underset{\displaystyle H}{\wedge}}{C}}-\overset{\overset{\displaystyle O}{\|}}{C}-O-Ag} \qquad \underset{\substack{\text{Glycocine hydrochlorate}}}{H-\overset{\overset{\displaystyle H}{|}}{N}-\overset{\overset{\displaystyle H}{|}}{C}-\overset{\overset{\displaystyle O}{\|}}{C}-O-H}$$

When treated with nitrous acid the amido-acids yield oxy-acids; thus the amido-fatty acids yield the oxy-fatty acids (Glycollic Acids, p. 14), by the replacement of the molecule NH_2 by the molecule OH.

8. *Glycocine* (glycocol, sugar of gelatin, amido-acetic acid), $C_2H_2(NH_2)O.OH$, does not occur, as such, in the body, but forms part of so-called conjugate acids, and exists in complex combinations in gelatin.

Glycocine when treated with nitrous acid yields oxy-acetic or glycollic acid. It can be prepared synthetically from chloracetic acid and ammonia. It unites with monobasic acids so as to form compounds, in which one H-atom of the NH_2 is replaced by the acid radical (the OH-group and the H-atom combining to form H_2O), thus:
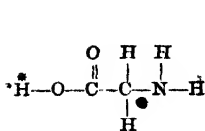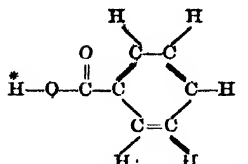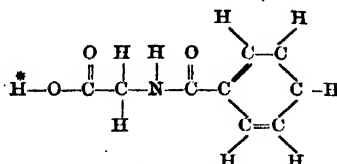
Glycocine	Benzoic acid (p. 17)	Hippuric acid
$C_2H_2(NH_2)O(OH)$	$CH(C_6H_5)O_2$	$C_9H_9NO_3$

The following are compounds which under hydrolytic influences combine with H_2O and split up into glycocine and an acid: they are called conjugate acids:

Glycocholic acid (see p. 16), $C_{26}H_{43}NO_6$, is a constituent of the bile.

Hippuric acid (Glyco-benzoic acid), $C_9H_9NO_3$, is a constituent of the urine of the herbivora, but occurs in every animal if benzoic or some other aromatic acids (cinnamic, mandelic, and chinic acids) have been taken with the food.

Other, so-called substituted, aromatic acids do not form hippuric, but corresponding acids.

9. *Alanine*, amido-propionic acid, $C_3H_4(NH_2)O.OH$, does not occur in the animal body.

10. *Butalanine*, amido-valerianic acid, $C_5H_8(NH_2) O.OH$, and

11. *Leucine*, amidocaproic acid, $C_6H_{10}(NH_2)O.OH$, are found in many constituents of the body, but, except in the pancreas, they are probably products of decomposition. When treated with nitrous acid, leucine yields oxycaproic acid or leucic acid (p. 14). Leucine is an important ingredient of the albuminous bodies.

12. *Serine* is probably amidolactic acid $C_3H_5 (NH_2)O_3$, and is obtained, in addition to leucine and tyrosine, by boiling silk-gelatine with acids.

When treated with nitrous acid it yields oxylactic acid, viz., glyceric acid.

13. *Cystine*, $C_3H_7NSO_2$, has been considered as serine, in which one atom of oxygen has been replaced by S, and has probably the same constitution.[1] It is a constituent of the kidneys, and is occasionally found in the urine and in urinary calculi.

14. *Taurine*, amido-ethyl-sulphonic acid, $SO_2(OH)$ $(C_2H_4.H_2N)$
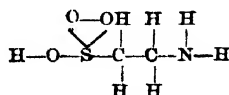
$SO_2(OH)_2$	$SO_2(OH)(C_2H_5)$	$SO_2(OH)(C_2H_4.H_2N)$
Sulphuric acid	Ethylsulphonic acid	Amido-ethylsulphonic acid or Taurine

[1] The formula of cystine is probably $C_3H_5NSO_2$; when decomposed by means of nitrous acid it does *not* yield glyceric acid, as would almost certainly be the case if it were derived from serine (Dewar and Gamgee).

This body occurs in the bile as a compound of cholic acid, similar to that of glycocine, viz. as *Taurocholic acid* ($C_{26}H_{45}NSO_7$); it is also present in a free condition in some glands.

15. *Tyrosine*, $C_9H_{11}NO_3$, is an amido-acid, whose constitution is not yet known, but which contains as its basis an aromatic residue ; it is found in small quantities together with leucine.   Like leucine, it is an important constituent of the albuminous bodies.

When heated with mercuric nitrate in presence of some nitrous acid, tyrosine yields a red colouration.

d. Amido acids, in which the hydrogen of the ammoniacal residue is itself substituted.

16. *Sarcosine*, methyl-amido-acetic acid or methyl-glycocine,

$$C_2H_2(NH[CH_3])O.OH,$$

is obtained when creatine is treated with alkalies, or synthetically by the action of methylamine on chloracetic acid (refer to p. 24, for the synthesis of Glycocine).   It is an isomer of alanine.

$C_3H_7NO_2$
Alanine

$C_3H_7NO_2$
Sarcosine
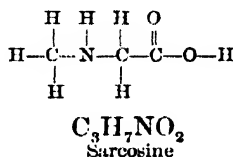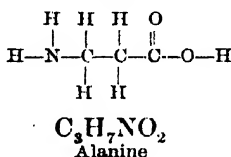
17. *Creatine*, methyl-guanidine-acetic acid, $C_4H_9N_3O_2$, is a constituent of the blood, the muscles, and the brain, &c.

Methyl-guanidine

Methyl-guanidine-acetic acid (Creatine)
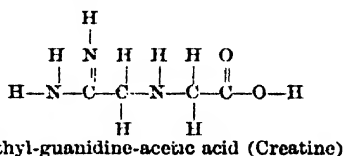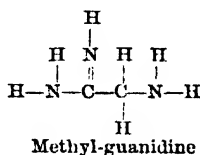
Creatine is obtained synthetically from cyanamide ($CN.NH_2$), and sarcosine ; one can in the graphic formula of creatine easily recognise, on the left, the residue of cyanamide, and, on the right, that of urea.

$$C_4H_9N_3O_2 + H_2O = C_3H_7NO_2 + CH_4N_2O.$$
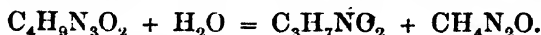
Actually, urea only differs from cyanamide in containing one molecule more of H_2O.

Cyanamide

Urea
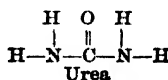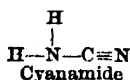
When oxidized (by means of mercuric oxide, peroxide of lead, &c.), creatine yields methyl-guanidine and oxalic acid, a decomposition which is intelligible enough when we consider that both methyl-guanidine and acetic

acid occur in creatine, and that oxalic acid is a doubly oxidized acetic acid (p. 15).

By other methods of oxidation, creatine yields methyl-parabanic acid, which is also an intelligible enough reaction.

e. Ammoniacal Derivatives of unknown Constitution.

18. *Uric acid*, $C_5H_4N_4O_3$, is a constituent, and in some classes of animals the principal constituent, of the urine.

The most probable view of the constitution of uric acid is, that.it is *tartronylcyanamide.*

$C_3H_2O_3(OH)_2$
Tartronic (or oxymalonic acid)

$C_3H_4O_3(NH_2)_2$
Tartronylamide

$C_3H_2O_3(NH.CN)_2$
Tartronyl-cyanamide (uric acid)
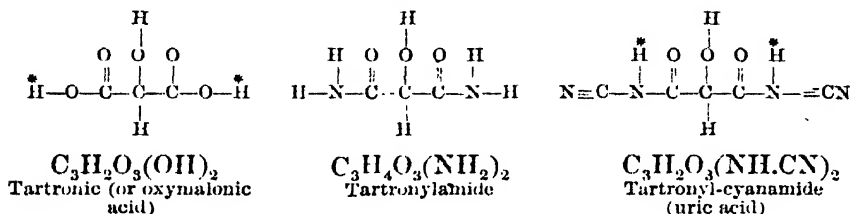
Uric acid is bibasic, as in it, as in compound ureas (p. 23), both the remaining H-atoms of the amide groups are replaceable by metals. Of the salts, of which the acid ones are, like uric acid itself, very slightly soluble in water, those of sodium and ammonium occur in man chiefly in pathological conditions.

By oxidation, uric acid yields:

a, in presence of acids, alloxan and urea :

$$C_5H_4N_4O_3 + H_2O + O = C_4H_2N_2O_4 + CH_4N_2O.$$
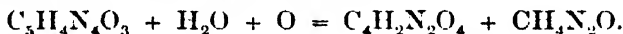
(Alloxan yields on further oxidation carbonic acid and parabanic acid, $C_4N_2H_2O_4 + O = CO_2 + C_3H_2N_2O_3$).

b, in presence of alkalies, allantoin ($C_4H_6N_4O_3$) and carbonic acid :

$$C_5H_4N_4O_3 + H_2O + O = C_4H_6N_4O_3 + CO_2.$$

c, when treated with nitric acid and evaporated to dryness, uric acid yields a golden-red residue, which is coloured purple-red (murexide, purpurate of ammonia) by ammonia and blue by potash.

19. *Xanthine*, $C_5H_4N_4O_2$, occurs in traces in many organs of the body and in the urine, and can artificially be obtained from hypoxanthine. A body isomeric with it is obtained from guanine.

20. *Hypoxanthine* or *Sarcine*, $C_5H_4N_4O$, occurs together with xanthine, into which it is converted by the action of oxidizing agents.

21. *Carnine*, $C_7H_8N_4O_3$, occurs in small quantities in extract of meat (Weidel); under the influence of bromine it is oxidized to hypoxanthine:

$$C_7H_8N_4O_3 + Br_2 = C_5H_4N_4O.HBr + CH_3Br + CO_2$$
<div style="text-align:center">Carnine   Sarcine hydrobromite   Methyl-bromide</div>

22. *Guanine*, $C_5H_5N_5O$, occurs in small quantities in the pancreas and liver, as well as in guano and the excrements of spiders.

When oxidized, guanine yields a body which is isomeric with xanthine (isoxanthine), nitrogen being evolved,

$$2\,C_5H_5N_5O + 3\,O = 2\,C_5H_4N_4O_2 + H_2O + N_2.$$
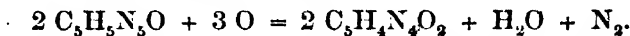
Other oxidizing agents split it up into carbonic acid, parabanic acid and guanidine,

$$C_5H_5N_5O + H_2O + 3\,O = CO_2 + C_3H_2N_2O_3 + CH_5N_3.$$
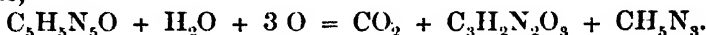
23. *Creatinine*, $C_4H_7N_3O$, is a constituent of urine.

Creatinine is a strongly alkaline substance; it forms a characteristic crystalline compound with chloride of zinc. It is an anhydride of creatine, from which it is easily obtained, and into which it is easily reconverted. The most probable view of the formation of this anhydride is shown in the accompanying formula.

$C_4H_9N_3O_2$
Creatine

$C_4H_7N_3O$
Creatinine
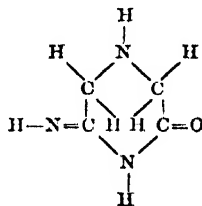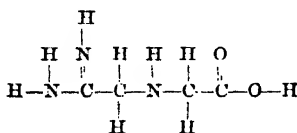
24. *Inosinic acid* $C_5H_8N_2O_6$, a constituent of muscles.

25. *Kynurenic acid* $C_{20}H_{14}N_2O_6$, occurs in the urine of dogs.

26. *Allantoin*, $C_4H_6N_4O_3$, is a constituent of the urine of the fœtus and the sucking infant. It is obtained by the oxidation of uric acid (see p. 27). Under hydrolytic influences allantoin splits into urea and allanturic acid $(C_3H_4N_2O_3)$; thus

$$C_4H_6N_4O_3 + H_2O = CH_4N_2O + C_3H_4N_2O_3$$
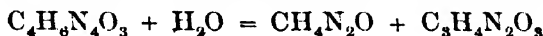
27. *Colouring matters.*—These substances, of which the best known are connected with the derivatives of ammonia, are in general crystallizable, and probably originate in one substance, which contains iron, and is called hæmatin. Some of these colouring matters contain no iron; these being the simpler, will be first treated of.

a. Bilirubin (biliphaein, cholepyrrhin, hæmatoidin), $C_{16}H_{18}N_2O_3$ (Städeler), the orange-red and crystallizable co-

louring matter of the bile, is insoluble in water, soluble in chloroform and in alkalies, with which it forms compounds, as if it were a monobasic acid. When oxidized it passes into biliverdin, and when more strongly oxidized into bilicyanin and choletelin. That it originates in hæmatin is proved by the fact that it, or at any rate a body exceedingly like it, is found in old extravasations of blood (hæmatoidin crystals).

In contact with nitric acid, which contains some nitrous acid, solutions of bilirubin show at their margins rainbow colourations, which are produced by the successive oxidations which take place. This (Gmelin's) test enables the smallest quantities of bilirubin to be detected.

b. Biliverdin ($C_{16}H_{20}N_2O_5$ = bilirubin + H_2O + O Städeler; $C_{16}H_{18}N_2O_4$ Maly) is formed when bilirubin is oxidized in air; it does not appear to occur in the organism: when treated with sulphurous acid it appears to be reconverted into bilirubin.

c. Bilifuscin $C_{16}H_{20}N_2O_5$ (= bilirubin + H_2O) and

d. Biliprasin $C_{16}H_{22}N_2O_6$ (= bilifuscin + H_2O + O) have been found in gall-stones in small quantities.

e. Bilicyanin (Heynsius and Campbell) is formed when any of the above-mentioned colouring matters are strongly oxidized; when present in acid solution its spectrum possesses an absorption band close to F; it is present in gall-stones.

f. Choletelin (Maly) is the last oxidation product of all the bile colouring matters.

g. Urobilin (Jaffe) is probably identical with hydrobilirubin, $C_{32}H_{40}N_4O_7$ (Maly), (a substance which can be obtained from bilirubin by reducing it in alkaline solutions), and with stercobilin (Vanlair and Masius), a constituent of fæces. This colouring matter occurs in urine, in bile, and in the intestinal contents; it possesses a broad absorption band in the green (at F), and when existing in alkaline solution together with chloride of zinc, it is strongly fluorescent.

h. Hæmatin is a product of the decomposition of the normal colouring matter of blood; its composition and properties will be described under Blood (Chap. I.).

i. Urinary colouring matters.—In the urine, several colouring matters have been found, of which some contain iron, others contain none; these substances do not crystallize, and their composition is unknown. One of these, urobilin (see above) occurs as a regular constituent in the bile and the intestinal contents. Blue colouring matters, which appear to belong to the indigo group, also occur in urine, but do not appear to exist in it preformed (see Chapter II).

k. Melanin is a black or brown colouring matter, which

contains iron, and is little known; it occurs in the lungs, the bronchial glands, the rete malpighii, the hair, the choroid, &c.

6. Complex Bodies of unknown Constitution.

As was formerly mentioned, the bodies which we have hitherto passed under review are to be considered as natural or artificial products of the decomposition of other much more complex bodies, in which the *molecules* of the simpler bodies, as OH, CH_3, NH_2, C_6H_5, occur in the most varied and intricate combinations.

Of these complex substances only a few can be obtained in a pure condition; the remainder cannot, either because they are too unstable, or because they are not crystallizable; with regard to the majority we do not therefore know even their composition by weight, much less their constitution.

The decomposition of these complex into more simple compounds is, nearly always, easily effected under so-called hydrolytic influences. One may (from the results of these decompositions) look upon them, either wholly or in great part, (1) as anhydrides or ethereal compounds, viz. as compounds of alcohol + alcohol − water, or alcohol + acid − water, or acid + acid − water, or (2) as amides, viz. acids + ammonia − water, or (3) as complex ureas, viz. as acids + urea − water, &c.

Meanwhile the hydrolytic products of the decomposition of many of these compounds are still too imperfectly known to allow of a complete insight into their structure. Besides, even were we sufficiently acquainted with these products, many difficulties would yet remain in the way of determining their constitution. We may illustrate these difficulties by referring to the anhydrides of sugar; if, for instance, we consider starch ($C_6H_{10}O_5$) to be derived from a single molecule of sugar, by the removal of one molecule of H_2O, there occur to us the most diverse possibilities as to the point in the body whence the H_2O was removed; the number of these possibilities increases enormously, however, if we assume that starch is derived from two molecules of sugar, $2H_2O$ being separated. We can thus explain that in the case of these more complex bodies there exist so many isomeric and polymeric compounds, possessed of almost identical properties, and whose true constitution is unknown.

The greater the number of atoms which combine to form a compound the greater becomes the complexity of its composition, so that elementary analyses are insufficient clearly to indicate its formula. The formulæ of the substances now to be treated of, are for this reason unknown to us.

We have to refer to the following groups of bodies:

Peptones and their Anhydrides (Albuminous Bodies and Albuminoid Bodies).

The peptones are formed within the body, by the hydrolytic decomposition of their anhydrides (see Digestion, Chap. III.), and apparently are soon reconverted into them. These anhydrides, the albuminous and albuminoid bodies, are very generally diffused throughout the body.

The hydrolytic products of decomposition of peptones are chiefly amido-acids, especially glycocine, leucine, tyrosine (pp. 24, 25, and 26). These cannot, however, be the only products of decomposition, for the majority of these peptones contain sulphur. It is unknown in what molecular combination the sulphur is contained, whether as sulphuric acid, as sulphuretted hydrogen, or as carbon disulphide. Even the nitrogen appears to be present in other states than in the amido-acids.

The various peptones differ in the relative quantities of the three amido-acids which they yield. Whilst all peptones yield leucine, gelatin-peptone furnishes only glycocine in addition : the remaining peptones, besides leucine, yield also tyrosine, in different quantities. It addition to tyrosine, when hydrolytic action is prolonged, other bodies possessed of a bad smell, and belonging to the indigo group, are obtained. The anhydrides yield, in the first place, peptones, and only afterwards the further products of decomposition.

1. PEPTONES.—The only peptone of which the percentage composition is approximately known is that which is obtained by the digestion of serum-albumin (C 51·37, H 7·25, N 16·18, S 2·12, O 23·11 per cent.)

The peptones are soluble in water, and partially soluble in alcohol (Brücke's 'Alkophyr'); they exert a left-handed rotation on the plane of polarisation. They differ from solutions of albumin in not being precipitated by heat, weak alcohol, dilute mineral acids, and divers metallic salts; they are, however, precipitated by corrosive sublimate, mercuric nitrate, silver nitrate, and chlorine. They possess three reactions, which will be described under Proteids. For the products of their hydrolytic decomposition see above—concerning their origin in the process of digestion, see Chap. III.

Proteids.

2. ALBUMINOUS BODIES (Protein bodies). These very numerous peptone-anhydrides occur in almost all the tissues and fluids

of the body dissolved in water, or more frequently in a glutinous (or swollen) state ; their solutions rotate the polarized plane to the left.   They are not crystallizable (all descriptions hitherto given of albuminous crystals are uncertain), and consequently cannot be obtained quite pure ; it is peculiarly difficult to free them from inorganic matters, with which they appear, partly, to exist in chemical combination.

By the action of heat and of mineral acids, and by the prolonged action of alcohol, they are converted into insoluble modifications (coagulated).

Seeing that by hydrolytic treatment the coagulated modification is, first of all, converted into the soluble, and that only then peptones are formed, it would appear that the coagulated modification is a further anhydride of the soluble.

The albuminous bodies form compounds with acids and alkalies, of which the former (acid-albuminates, syntonin) are precipitated by alkalies, the latter (alkali-albuminates, casein) by acids.

Oxidizing and other reagents, which act energetically upon the albuminous bodies, yield, by their action upon them, amido-acids (see above): glycocine, leucine, tyrosine; further, volatile fatty acids, benzoic acid, hydrocyanic acid ; aldehydes of the fatty acids, and of benzoic acid, &c., and it is even said urea. They thus contain nitrogen in ammonia and cyanogen molecules.

Nitric acid colours the albuminous bodies (and the peptones likewise) of a yellow colour (xantho-proteic reaction), and the addition of alkali changes the colour to red.   Mercuric nitrate, in the presence of a little nitrous acid, at 60° C., colours the albuminous bodies red (Millon's reaction).   This reaction, which agrees with that of tyrosine, probably depends upon an intermediate formation of tyrosine.

With cupric sulphate and potassium hydrate the albuminous bodies yield a violet solution.

All these three reactions may be employed in the detection of the albuminous bodies.

The origin of the albuminous bodies is not known with certainty ; but it is very probable that they may be regenerated within the animal body, by synthetic processes, from peptones, and perhaps even from the still simpler products of decomposition formed during the digestion of the albuminous matters of

the food (Chap. III. and V.) The latter are derived in the first instance from plants, which are the only constructors of albumin.

Equally little is known of the ultimate end of the albuminous bodies in the organism. It would appear as if the so-called *albuminoid* bodies were their closest derivatives. In their more thorough decomposition in the organism, the nitrogen probably passes into amido-compounds, of which the most completely oxidized, as urea, are excreted. It is, however, very probable, from their composition, that fats, glycogen, and sugars take their origin in the albuminous bodies, and in support of this view there are weighty physiological facts. Conversely, it appears that synthetic processes of a higher order occur in the organism, whereby albuminous bodies form still more complex compounds (see below, p. 36).

The various albuminous substances of the body possess nearly the same percentage composition : C 52·7 — 54·5, H 6·9 — 7·3, N 15·4 — 16·5, S 0·8 — 1·6, O 20·9—23·5 per cent. By hydrolytic processes they yield ¼ to 2 per cent. of tyrosine and from 10—18 per cent. of leucine. They are chiefly distinguished from one another by the circumstances of their precipitation and coagulation.

The most important are :—

a. ALBUMIN, which occurs in blood-serum, in white of egg (somewhat modified), and in most tissue-juices. It coagulates in neutral or acid solutions at temperatures varying from 60—70° C.

The casein of milk is a potassium albuminate, but does not coagulate when simply heated ; it does so only when an acid is added. It is precipitated by most acids.

b. GLOBULIN is a constituent of the blood and of many tissues ; it is precipitated from its solutions by acids, even by carbonic acid, the precipitate being dissolved by the subsequent passage of oxygen ; it is probably an albuminate of potassium. Many different forms of this body exist, and these are, in part, designated by the term ' paraglobulin ' (Chap. I.)

c. FIBRIN, the stringy constituent of coagulated blood ; a body which separates as the result of the inter-action of two kinds of paraglobulin (the fibrinoplastic and fibrinogenous substances) (Chap. I.). When heated, fibrin assumes the characters of a coagulated albuminous body.

D

d. MYOSIN, the coagulum of muscles which have sponta-
neously passed into the state of ' rigor ' (Chap. VIII.)

The syntonin of muscles is merely an acid albuminate which is produced
by acid which is formed in muscle or which has been employed in its extrac-
tion (p. 32).

3. ALBUMINOID BODIES.—These substances, which occur as
the principal constituents of many tissues, and approach the
albuminous bodies in composition (although some of them
contain no sulphur), are looked upon as their nearest deriva-
tives. We do not know by what processes they arise from
them : whether by oxidation, or, on the contrary, by synthesis, or
in any other way.

They differ from one another much more than the albumi-
nous bodies, and, if we except their colloidal character, *i.e.* their
inability to crystallize and to form true solutions, they possess
no common character. Under hydrolytic influences they furnish
the same products as the albuminous bodies, viz. leucine and
tyrosine, in large quantities. One of these bodies, chondrin,
which is said to yield grape sugar when it is boiled with dilute
sulphuric acid, must be a glucoside, and should therefore be
separated from the other substances.

The most important albuminoid bodies are—

a. Mucin, (C 52·2, H 7·0, N 12·6, O 28·2 per cent.) forms a
viscid fluid with water (mucus), which is precipitated by a little
acetic acid, and by excess of alcohol. It occurs in mucous
secretions, and in gelatinous connective tissue (Wharton's jelly,
&c.) Besides leucine, it yields much tyrosine.

b. Glutin, gelatin (C 50·4, H 6·8, N 18·3, S + O 24·5) is
extracted from nearly all the connective tissues (bones, liga-
ments, skin) by boiling them with water. Gelatin swells in
cold water ; by boiling, a solution is obtained which again
gelatinizes on cooling. On prolonged boiling it splits up into
a non-gelatinizing peptone, which also is a product of digestion.
Hydrolytic treatment furnishes leucine, glycocine, and ammonia,
but no tyrosine.

c. Sericin, or silk–gelatine ($C_{15}H_{25}N_5O_8$?) is a constituent of silk.

d. Keratin (C 50·3 — 52·5, H 6·4 — 7·0, N 16·2 — 17·7, S 0·7
— 5·0, O 20·7 — 25·0 per cent.) is the residue left when the so-
called horny tissues have been treated with ether, alcohol, water
and acids : it is a substance only soluble in hot alkalies, and

which swells up in cold alkalies. It yields 10 per cent. of leucine, and 3·6 per cent. of tyrosine.

e. Elastin (C 55·5, H 7·4, N 16·7, O 20·5 per cent.) is the residue left after the removal of all soluble matters from connective tissue; it is the *characteristic substance of all elastic tissues.* It is insoluble in all agents which do not decompose it.

It yields much leucine (36—45 per cent.), but little tyrosine ($\frac{1}{8}$ per cent.)

f. Fibroin (C 48·6, H 6·5, N 17·3, O 27·6 per cent.), is the chief constituent of silk, and is soluble in concentrated acids and alkalies.

g. HYDROLYTIC FERMENTS are bodies which, by an action which is not yet understood, cause a decomposition of bodies which are in proximity to them, without being themselves consumed; the bodies which are decomposed combine with the elements of water.

Formerly these animal ferments were considered to belong to the albuminous bodies; the best known among them do not, however, possess the characters of albuminous substances, which, however, often adhere mechanically to them.

In order to separate many ferments in a pure condition we may avail ourselves of their property of adhering to bulky precipitates, as to the precipitates which are produced when solutions of cholesterin or collodion are added to fluids which contain them.

The animal body contains the following hydrolytic ferments :—

a. AMYLOLYTIC, OR SUGAR-FORMING FERMENTS, which convert starch, glycogen, &c. into sugar, with absorption of water; these ferments are present in saliva, pancreatic juice, in the liver, and many other organs.

β. FAT-DECOMPOSING FERMENTS, which cause fats to combine with the elements of water and to decompose into fatty acids and glycerin; a ferment of this class appears to exist in the pancreatic juice.

γ. FERMENTS WHICH DECOMPOSE THE ALBUMINOUS BODIES : these ferments which exist in the gastric juice (pepsin), and in pancreatic and intestinal juices, convert soluble and coagulated albuminous bodies into peptones, and then into leucine, tyrosine, &c.

No other but hydrolytic ferments have yet been discovered in the body.

2. BODIES MORE COMPLEX THAN THE ALBUMINOUS SUBSTANCES.—We can only certainly assume the existence of bodies of this class from the fact that when they are decomposed albuminous bodies are liberated.   To this group belong—

1. *Hæmoglobin*, the red crystalline colouring matter of the blood corpuscles, which is likewise contained in small quantities in serum and in the muscles.   Its properties will be described in the chapter on Blood.

2. *Vitellin*, a crystalline body which, when decomposed, yields albumin and lecithin.   It is a constituent of the yolk of eggs.

3. *Ichthin*, a body which apparently has a similar constitution to vitellin, and which is found in the ova of fishes (ichthidin and emydin are bodies of the same kind).

With the exception of the above, no other bodies having a more complex constitution than the albuminous have yet been demonstrated to exist.   Nevertheless, it appears in the highest degree probable that such a body exists in the muscle, one of whose products of decomposition is myosin.

3. GLUCOSIDES WHICH CONTAIN NITROGEN.—The following nitrogenous glucosides have been discovered in the human organism.

1. *Protagon*, which is a glucoside of lecithin, occurs as a constituent of the brain, of the blood, and probably also of other organs which contain lecithin.   Under the action of hydrolytic ferments, it yields grape sugar and the decomposition products of lecithin (choline, glycerinphosphoric acid, &c.); its formula has not been determined.[1]   It is insoluble in water, but swells into a viscid mass; it is soluble in alcohol and warm ether.

2. *Chondrin* (C 49·9, H 6·6, N 14·5, S 0·4, O 28·6 per cent.), is extracted from hyaline cartilage and the covering of the holothuria by boiling with water; in its external characters it resembles gelatin.   Under hydrolytic treatment it furnishes leucine and grape sugar (the latter fact is disputed).

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[1] According to recent researches (Hoppe-Seyler and Diaconow) protagon appears to be a mixture of lecithin and cerebrin.   *Cerebrin* (W. Müller), $C_{17}H_{33}NO_3$ (?), is a glucoside, and possesses the property, ascribed to protagon, of swelling when acted upon by water.   When decomposed by mineral acids it yields, in addition to other bodies which have not yet been investigated, a sugar-like body which rotates the plane of polarization to the left.

3. *Chitin*, a nitrogenous glucoside, is contained in the shell or exoskeleton of arthropoda.

4. *Hyalin* is a nitrogenous glucoside found in the cysts of echinococci.

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In the foregoing pages the chemical constituents of the animal body have been classified according to their chemical affinities. Other methods of classification are based on the origin of these substances in the body, but they are necessarily unsatisfactory, in consequence of the slight acquaintance which we possess with the chemical processes of the organism.

The basis of the most commonly adopted arrangement is the fact that from the albuminous bodies, the carbohydrates and the fats, which form the chief organic food of the body, all its constituents are derived. The changes which each substance undergoes in its conversion into a formed element of the body are included in the term *assimilation*, or 'progressive metamorphosis,' whilst the further changes which end in excretion are included in the term 'retrograde metamorphosis.' Processes of oxidation and decomposition play the principal part in bringing about the latter; complicated breaking up into more and more simple bodies, the chief representatives of which are carbonic acid, water, urea, sulphuric and phosphoric acid.

The chemical processes which are concerned in the so-called 'progressive metamorphosis,' and which lead to the formation of albuminoid bodies, of hæmoglobin, of protagon, &c., are altogether unknown to us, although we may doubtless conclude that in their production synthetic processes play some part.

CHAPTER I.

THE BLOOD AND ITS CIRCULATION.

THE material interchanges which take place between the constituents of the body and the external world, and between these constituents themselves, occur through the medium of a fluid which is in perpetual contact with the remotest parts of the body, as well as with those apparatuses which are to be considered as the portals by which the body communicates with the exterior; that fluid is the blood.

The blood receives directly from the external world oxygen and nutritive matters, and from it the individual *tissues* obtain these substances. The latter, again, rarely give up their excrementitious products *directly* to the external world, but pour them, first of all, into the blood, which throws them out of the body at certain destined places. The blood, moreover, is continually taking up substances which have undergone changes in different localities, and deposits them, for further use, elsewhere.

Every particle of the body which plays a part in its chemical changes must therefore, repeatedly, presumably very frequently, become the constituent of a very voluminous fluid (the blood), in which it mixes with innumerable other substances, so that its further progress outwards depends upon the accident of the place at which it again leaves the mass of the blood.

It is therefore expedient, in the exposition of the chemical changes which occur in the body, to consider the blood as its natural centre, and to classify the various processes as sources of expenditure or gain to the blood, before treating of the interchanges between the matter of the whole organism and the external world.

I. THE BLOOD.

Human blood is a red fluid, opaque even when in very thin layers, and possessed of an alkaline reaction. It consists of a yellow alkaline liquid (liquor, or plasma, sanguinis), and small microscopic bodies, the blood corpuscles, which are suspended in the fluid in large numbers (4 to 5·5 millions in one cubic centimetre; Welcker), and are in close contact with one another. These are mostly red, but a small number (1 in 500 or 1 in 300, Welcker—in the splenic veins, however, 1 in 70, Hirt) of colourless corpuscles are mixed with them.

To test the alkaline reaction of blood the mere employment of litmus paper is not sufficient; either the colourless diffusate obtained by means of a porous septum and distilled water is tested (Kuhne), or a drop of blood is placed on litmus paper which has been previously moistened with a solution of common salt (Zuntz).

Red Blood Corpuscles.

In man, the red blood corpuscles have the form of circular, biconcave discs; their greatest diameter averages $\frac{1}{126}$mm. They are uniformly coloured red. They are very soft, ductile, and elastic; neither membrane nor nucleus can be detected, so that they cannot be designated cells.

The blood corpuscles of mammalia, with the exception of the elliptical ones of the camel, are similar to those of man; in birds they are elliptical and biconvex; in amphibia elliptical. flat, and very large (in Proteus the diameter is actually $\frac{1}{16}$mm); in fishes they are mostly of a rounded elliptical form. In birds, amphibia, and fishes, they have *nuclei*. In the invertebrata red blood corpuscles are only present in a few classes. Almost all invertebrata, and amongst vertebrata Amphioxus lanceolatus, have colourless or yellowish blood, with colourless corpuscles of various shapes; a few, however, have red blood with colouring matter similar to that of vertebrata.

The specific gravity of blood corpuscles is somewhat greater than that of the plasma; for if not prevented (by coagulation, &c.) they sink to the bottom of blood which is undisturbed. When blood is at rest, the red corpuscles have a tendency to aggregate into piles, like *rouleaux* of coins. The cause of this phenomenon is unknown.

The presence of red corpuscles is the cause not only of the red colour, but also of the opacity of the blood. By a variety of means the red colouring matter can be extracted from the blood

corpuscles, when it dissolves in the plasma and colours it red; the blood becomes in consequence transparent when examined in thin layers ('lake-coloured,' Rollett), but at the same time, darker, owing to the absence of reflection from the concave red disks. Conversely, the blood becomes of a brighter red when the blood corpuscles are shrivelled up by the addition of salt, so that the reflected light becomes more concentrated. The corpuscles in the process of decolourization swell up from their margins (Hermann) and finally become globular; the decolourized and very pale residue of the corpuscles is called the *stroma* (Rollett).

The means of discolourizing the blood corpuscles, previously referred to, are: dilution of the blood with water: alternate freezing and thawing of the blood (Rollett): the transmission of electric shocks (Rollett): removal of the gases of the blood (see below): treatment with salts of the bile acids (v. Dusch), ether (v. Wittich), chloroform (Böttcher), small quantities of alcohol (Rollett), or carbon disulphide (Hermann). All these processes, except the first named and the removal of the gases of the blood, not only effect the discolourization of the corpuscles, but subsequently lead to the solution of the stroma in the plasma, a glutinous nucleus being sometimes left.

By the action of boracic acid on the nucleated corpuscles of amphibia, a red mass containing the nucleus is separated from the residual colourless stroma; we must therefore admit that the former contractile mass (the Zooid) is infiltrated in the pores of the colourless stroma (the Oecoid; Brucke).

A similar deportment is observed in the case of the non-nucleated blood corpuscles of mammalia (Roberts, Stricker). Some consider these separations which are produced in numerous other ways, as the results of coagulation (Rollett).

The chemical constituents of the red blood corpuscles are:

1. A red colouring matter containing iron, called Hæmo-globin (syn. hæmatoglobulin, hæmatocrystallin), having approximately the following percentage composition: C 54·0, H 7·25, N 16·25, Fe 0·42, S 0·63, O 21·45.

It is slightly soluble in water, but much more readily soluble in weak alkaline solutions. It is not known whether hæmoglobin impregnates the colourless residue of the zooid of the blood corpuscles, or whether it exists in a state of chemical combination with it.

Hæmoglobin is a coloured albuminous compound, and is therefore a body of most complex structure. It readily splits up into an albuminous body, apparently closely connected

to globulin (although, unlike the latter, it is not dissolved by oxygen), and a colouring matter, hæmatin. This decomposition is effected by all agents capable of coagulating or precipitating albumin (heat, alcohol, mineral acids), and, besides, by the weakest acids (even by carbonic acid in the presence of much water), and by strong alkalies. Different red-blooded animals possess different kinds of hæmoglobin, which have hitherto only been found to differ in their crystallization.

Crystals of hæmoglobin, the so-called *blood-crystals*, occur principally in the form of rhombic prisms or tablets; rarely, as in the blood of the guinea-pig, in the form of rhombic tetrahedra. These crystals may be obtained by destroying the blood corpuscles (by means of water, ether, salts of the bile acids), and evaporating or cooling the lake-coloured fluid which results. Crystals are easily obtained from the blood of dogs, horses, guinea-pigs, and birds; with difficulty or not at all from that of oxen and pigs.

The coloured product of the decomposition of hæmoglobin, Hæmatin ($C_{68}H_{70}N_8Fe_2O_{10}$? Hoppe-Seyler), which does not occur uncombined in the body, is a crystalline colouring matter, which, when dried, has a bluish-black colour and a metallic lustre; it is insoluble in water and alcohol, but soluble without decomposition in aqueous or alcoholic solutions of acids and alkalies. Its acid solutions are brown, its alkaline solutions are dichroic, appearing green in thin, and red in thicker layers.

Solutions of hæmatin, when examined with the spectroscope, exhibit an absorption band in the red, the position of which is different in acid and alkaline solutions. When treated with reducing agents two new absorption bands, situated close to each other in the yellow, make their appearance; these are not to be confounded with the two bands of O-hæmoglobin (see below). Hæmatin crystallizes from solutions in glacial acetic acid in the form of rhombic plates, which in the presence of chlorides are composed of hydrochlorate of hæmatin (Hoppe-Seyler); these so-called hæmin-crystals may serve for the detection of blood (Teichmann).

By the action of concentrated mineral acids iron is separated from hæmatin; the resulting colouring matter bears the name of 'iron-free hæmatin' (Mulder and von Goudoever), hæmatoporphyrin ($C_{68}H_{74}N_8O_{12}$? Hoppe-Seyler), hæmatoin (Preyer).

According to recent accounts (Hoppe-Seyler), when hæmoglobin is decomposed in the absence of air, a purple body, with four absorption bands, 'hæmochromogen,' is formed; the action of oxygen immediately converts it into hæmatin.

In the organism hæmoglobin gives rise to coloured products other than the artificial ones, as hæmatoidin, bilirubin, &c. (For these consult Chapter II. under the heads of Bile,

Urine, &c.). For the deportment of hæmoglobin towards gases, and for its optical properties, see below.

2. An albuminous body precipitable by carbonic acid, but soluble on the passage of air through the fluid, *globulin.*

The nuclei of the blood corpuscles consist of a substance containing mucin (Brunton).

3. Small quantities of substances soluble in ether: fats, soaps, cholesterin, protagon, and its products of decomposition (lecithin, glycerin-phosphoric acid, &c.).

4. Salts, especially compounds of potassium, and of phosphoric acid.

5. Water.

6. Gases.

Colourless Blood Corpuscles.

The colourless blood corpuscles (lymph corpuscles) are globular, nucleated cells, with a somewhat granular, mulberry-shaped surface; they are larger than the red corpuscles, having a diameter of about $\frac{1}{100}$mm. They show the greatest resemblance to the cells of the lymph, from which they are derived (Chapter III.). At the temperature of the body these cells, which are destitute of a cell wall, exhibit lively movements, throwing out processes and drawing them in again, whereby they can drag into their interior foreign particles (compare Chapter VIII.); these cells also possess the power of subdividing (Klein). Their chemical composition has not yet been exactly determined; it is probably very similar to that of the red corpuscles without the pigment. There are grounds for believing (Chapter V.) that the colourless blood corpuscles are precursors of the red, as transition forms between white and red corpuscles are found in certain situations (for example, in the blood of the splenic veins).

Blood Plasma or Liquor Sanguinis.

For the separation of the plasma of the blood see below (under 'Dying of the Blood'). The reaction of blood plasma is, like that of blood itself, alkaline. The chemical constituents of the plasma are:

1. Water, about 90 per cent.

2. Proteids, viz.:

    a. Albumin (precipitated by heat).

    β. Sodium albuminate ('serumcasein,' precipitated by acids).

    γ. The substances which form fibrin during coagulation of the blood (see below).

The greater portion of the albuminoid substances consists of albumin: altogether they form from 8–10 per cent. of the plasma.

3. Creatine, hypoxanthine, and urea: also at times hippuric and uric acids, in very small quantities.

4. Grape sugar, in small quantities, varying according to the situation (see Chapter V.).

5. Fats, soaps, fatty acids, cholesterin, lecithin. The fat is partly dissolved by the soaps, and partly exists as an emulsion, but always in a small, though varying, quantity ($0.1 - 0.2$ per cent.).

6. An odoriferous principle peculiar to each kind of blood.

7. A *yellow pigment.* (The serum also often contains hæmoglobin, but this may be only an impurity, caused by disintegrated blood corpuscles.)

8. Salts, with a preponderance of salts of sodium, chlorides, and carbonates; therefore more especially common salt and carbonate of sodium.

9. Gases (see below).

With the exception of the bodies included under 2, the above-named constituents form also the constituents of the serum—that is, of the liquid obtained after the coagulation of the blood or plasma (see below).

The Gases of the Blood.

The gases contained in blood are oxygen, carbonic acid, and nitrogen which are partly absorbed, and partly in loose chemical combinations (Magnus, Lothar Meyer, Ludwig).

The fundamental law of the absorption of gases by liquids (Henry's, Dalton's, and Bunsen's law) may be expressed as follows:—The unit of volume of a liquid at a given temperature absorbs a definite volume of a gas; the latter is designated the *coefficient of absorption of the liquid for the gas.* The coefficient of absorption decreases as the temperature increases, according to a law which varies for each liquid and gas; at the boiling point of the liquid the coefficient of absorption is equal to 0.

The *volume* of gas taken up, therefore the absorption coefficient, is inde-

pendent of the pressure, whilst the *weight* of the gas taken up by a fluid is directly proportional to it.

As different gases existing in a gaseous mixture exert no pressure upon one another, we must in the preceding sentence understand pressure to signify the partial pressure of the particular gas. Thus water absorbs only as much oxygen from the atmosphere as corresponds to the partial pressure of the oxygen contained in it, viz. about $\frac{760}{5} = 152^{mm}$ Hg.

Absorbed gases can therefore be expelled from a liquid, 1. By placing it in a vacuum which is being continually renewed. 2. By placing it in a space which is free from the gas to be expelled, and which is maintained free. 3. By raising the temperature of the liquid to boiling point.

Certain gases form chemical compounds with certain bodies (in the relations of their equivalents), which, however, undergo DISSOCIATION when they are placed in a space where the partial pressure of the gas falls below a certain limit. This minimum pressure, which is an essential condition to the persistence of the combination, is, for each special case, a *constant*, which, still, like the coefficient of absorption, decreases as the temperature increases. From these loose chemical combinations the gas can, therefore, be driven as from simple solutions (viz. by the vacuum, by foreign gases, or by the action of heat). These loose compounds of gases are distinguished, however, from simple solutions, in that by increasing the partial pressure of the gas beyond a certain limit, the quantity taken up by the liquid no longer increases.

There are some bodies which form loose chemical compounds with gases dissolved in a liquid, so that the solution may contain a chemical compound of the gas as well as a portion simply dissolved. In such a case the weight of the gas dissolved is partly proportional to the pressure, and partly independent of it.

The quantity of gas by weight taken up by a solution is dependent on the partial pressure of that gas outside the fluid, because each gas which is dissolved by a liquid possesses, at the surface of the latter, a tension, in virtue of which it tends to escape. If this tension is equal to the partial pressure of the gas in the space above the liquid, equilibrium is established ; if it is greater or less, a passage of gas outwards or inwards occurs, until a condition of equilibrium is attained. In the condition of equilibrium, which is always established sooner or later, (and which is hastened by shaking together the liquid and gas) the partial pressure of each gas in the space surrounding the liquid expresses directly the tension of the same gas in the fluid. If we carry the idea of tension into the statement of the laws which have been previously announced, these may be expressed as follows. 1. In the case of purely physical absorption, the tension of a dissolved gas is (*a*) dependent upon the nature of the fluid and the gas, (*b*) proportional to the amount, by weight, which has been taken up, (*c*) dependent upon the temperature—with which it, in general, increases. 2. If a fluid contain a body which forms a loose chemical compound with a gas, the tension is not proportional to the total quantity of gas taken up, but only to the excess above the quantity which is required to saturate the combining body ; if the body, on the other hand, is not saturated, fresh absorption of the gas leads to no

increase of tension, but the latter remains equal to the above-mentioned minimum pressure, which, however, varies with the temperature.

In order to separate, whether for qualitative or quantitative determination, the gases, contained in a fluid, *e.g.* in blood, one of the three above-mentioned means may be employed, or a combination of several (as boiling in the vacuum of an air-pump or in the Toricellian vacuum). In consequence of the consumption of oxygen which goes on in the blood immediately after its withdrawal from the body (see below, under Dying of the Blood), we must, if we wish to ascertain the real amount of its gases, either separate these immediately after it has left the body, or we must preserve the blood in ice until the time when the gases are separated.

In order to determine whether gases are in a state of simple solution or of loose chemical combination in the blood, either absorption experiments must be made under different pressures, with blood which has been freed from gases, or we must make determinations of tension. The methods for effecting the latter, which are of special importance in reference to the chemistry of respiration, will be given in Chapter IV.

1. *Oxygen* gas is found in arterial blood (see below), on an average, in the proportion of 16·9 volumes per cent. (the gas being calculated under a pressure of 1 mtr. and 0° C.), (Pflüger): the amount of oxygen in venous blood varies greatly (Chapter IV.); in venous blood from muscles in a state of rest the amount was found to be only 5·96 volumes per cent., taking an average of 5 determinations. The deportment of blood, which has had its gases removed, towards oxygen, shows that the latter is not merely absorbed by the blood, *but for the most part chemically combined with it.* The amount (by weight), of the oxygen taken up by blood is almost entirely independent of pressure, and does not therefore follow Dalton's law. But if the blood corpuscles are removed, and simple blood plasma be taken, or (since the latter is difficult to obtain, and immediately coagulates, whilst as regards combination with O the fibrin-formers may be considered as unimportant), instead of plasma, plain serum (page 50), be agitated with oxygen, the gas is merely absorbed (L. Meyer). It follows from this that the oxygen of the blood is chemically combined with a substance contained in the blood corpuscles, but is only absorbed by the plasma or serum (that is, by the water they contain, for serum absorbs just so much oxygen as pure distilled water).[1] This proposition must likewise be applied to the oxygen normally present in the blood.

[1] It has been stated (Fernet) that plain serum likewise takes up a certain amount of oxygen, independently of pressure; this result is probably owing to the presence of a slight amount of hæmoglobin in the serum.

Hæmoglobin is the substance which forms the loose chemical compound with oxygen, and it likewise possesses the property of combining with some other gases in constant proportions : 1$^{grm.}$ of hæmoglobin combines with 1·2 — 1·3 °CC of O (measured at 0° C and 1 meter pressure). The compound which we may designate O–Hæmoglobin is crystallizable and somewhat less soluble than pure hæmoglobin. Its solutions are of a lighter red than those of the latter; they are not dichroic, whereas hæmoglobin, which is free from gases, and which we may term reduced hæmoglobin, appears green when examined in thin layers. Solutions of O–Hæmoglobin exhibit, when examined by means of the spectroscope, two absorption bands situated in the green portion of the spectrum. Solutions of reduced hæmoglobin, on the other hand, exhibit a single, less defined, band, which occupies the interval between the two first bands.

Oxygen can be removed from its combination with hæmoglobin not only by the means formerly referred to, but also readily by the action of many reducing substances, as by ammonium sulphide, by alkaline solutions of ferrous salts, by iron, by nitric oxide. The minimum pressure required for the persistence of the compound of O + Hæmoglobin, viz. the tension of the oxygen of the blood, is dependent on the temperature, but its absolute value is still unknown.

In addition to oxygen, hæmoglobin can also combine chemically with carbonic oxide (L. Meyer) and with nitric oxide (Hermann), in the same proportions by volume, therefore in the same equivalent proportions. Of these compounds, that with oxygen is the least stable, so that the oxygen may be expelled from its combination with hæmoglobin by carbonic oxide, and the latter, in its turn, by nitric oxide. Even the two latter compounds are to be designated as unstable, seeing that according to recent investigation (Donders, Zuntz, Podolinski) they are also capable of decomposition by physical means; the pressure at which they decompose is, however, much lower than in the case of the oxygen compound. These CO- and NO-compounds are, like the O-compound, not dichroic, and they possess two absorption bands, which in the carbonic oxide compound are somewhat differently situated from those in the other two analogous compounds. When O-Hæmoglobin is decomposed by means of acids, the oxygen is not liberated and cannot be pumped out; it must, therefore, enter into chemical combination with one of the products of decomposition (L. Meyer, Zuntz, Strassburg).

Seeing that the behaviour of the blood as a whole towards oxygen (carbonic oxide, &c.), as well as its optical properties and the dependence of these upon the gas contained in the blood, is

exactly the same as that of a solution of hæmoglobin, and, further, as blood when saturated with oxygen takes up exactly as much of that gas as corresponds to the amount which its hæmoglobin can combine with, it follows that all the loosely combined oxygen of the blood is linked to hæmoglobin.

The oxygen of the blood is given up so readily to oxidizable substances that it has been thought to be present in the form of *'active oxygen'* or *'*ozone,' O_3. The following properties of blood appear to favour this view. 1. Both the blood-corpuscles and hæmoglobin are so-called 'ozone-transferrers,' that is, they possess the power of immediately transferring ozone·from substances in which it is present (as turpentine which has been kept for a long time) to readily oxidizable substances (ozone reagents, such as tincture of guaiacum, which becomes blue by oxidation, Schoenbein, His); for this reaction the presence or absence of oxygen in the blood is of no importance (for instance, it may be saturated with CO). 2. Blood and hæmoglobin can themselves ozonize oxygen, so that in presence of air they can cause guaiacum tincture to become blue (A. Schmidt); if the blood itself contains oxygen, the presence of air is not necessary; it is necessary if the blood has been saturated with CO (Kühne and Scholz). On the activity of its oxygen depends the decomposition of sulphuretted hydrogen by blood. It is therefore very probable that the oxygen naturally contained in blood is present in the form of ozone, or in some similar condition.

2. *Carbonic acid* is found in arterial blood on an average in the proportion about 30 vols. per cent.: venous blood from muscles at rest yields about 35 per cent. A portion of the carbonic acid can only be driven out by acids; it is therefore in stable chemical combination. The carbonic acid removable by the pump may either be merely absorbed, or partly in very weak chemical combination. A weak chemical combination may take place either, with 1, the carbonate of sodium of the plasma, 2, the phosphate of sodium of the plasma (Fernet), 3, through as yet unknown combinations in the blood corpuscles (Pflüger and Zuntz, Ludwig and A. Schmidt). Since solutions which contain carbonic acid, either absorbed or in weak combinations, give an acid reaction, the fact of the alkaline reaction of the blood would appear opposed to the view of the carbonic acid being present in other than a stable combination (Preyer), were it not that blood still gives an alkaline reaction when *saturated* with carbonic acid (Pflüger and Zuntz).

Since the phosphate of sodium in blood ash is derived almost entirely from burnt lecithin, the second combination referred to is probably only very slightly operative (Hoppe-Seyler and Sertoli). Since, moreover, the

serum takes up carbonic acid independently of pressure, just like the blood itself, a part, at least, of the chemically combined carbonic acid must be in the serum (that is, in the plasma), probably in the form of bi-carbonate (see above No. 1). That a part of the carbonic acid is combined in the blood corpuscles (see No. 3) is shown by the fact, that blood contains scarcely less carbonic acid than a similar volume of serum (Ludwig and Schmidt), and moreover that the absorption of carbonic acid by blood and by serum under increasing pressure obey different laws (Pflüger and Zuntz.)

Carbonate of sodium is changed by the addition of carbonic acid into the bi-carbonate $CO_3Na_2 + CO_2 + H_2O = 2\ CO_3NaH$; the neutral salt is again formed along with free carbonic acid by the employment of the means used to drive out the gases. Neutral phosphate of sodium takes up carbonic acid in a similar manner (one equivalent of acid to two equivalents of salt), (Fernet), forming an acid phosphate and neutral carbonate: $2\ PO_4Na_2H + CO_2 + H_2O = 2\ PO_4NaH_2 + CO_3Na_2$ (Hermann). The means used to drive off the gases break up these combinations, giving off CO_2 and again forming the neutral salt.

3. Blood contains from 1–2 vols. per cent. of *Nitrogen.* A small portion of this gas also is probably chemically combined, being most likely contained in the blood corpuscles (Fernet, Setschenow).

When heated (Thiry) or merely allowed to stand (Brücke) the blood gives off traces of ammonia, probably arising from the decomposition of some ammoniacal salt contained in the blood (Kühne and Strauch); no proof has, however, yet been obtained of the presence of such a salt in the blood (Brücke). The addition of oxygen favours the development of ammonia (Exner).

Blood which has been deprived of its gases is very dark (almost black), dichroic, and, in consequence of the destruction of the blood-corpuscles, lake-coloured.

Different kinds of Blood.

The composition of the blood is not the same throughout the whole body. The greatest difference is observed between *arterial* blood (viz. that which is contained in the systemic arteries, the left side of the heart, and the pulmonary veins), and *venous* blood (viz., that of systemic veins, the right side of the heart, and the pulmonary arteries), and consists principally in the amount of gases contained, and in the colour. Arterial blood contains more oxygen (on the other hand, less carbonic acid) than venous, and has a brighter (scarlet) colour; it does not display the dichroism of the latter. This difference in colour is closely connected with the difference in the amount of oxygen;

for on shaking up dark-coloured blood with oxygen (or with atmospheric air), it becomes bright red, and bright red blood becomes dark-coloured when shaken with other gases (except carbonic oxide, page 46).

Moreover, arterial blood contains more water, fibrin, salts, sugar, and extractive matter than venous, but on the other hand fewer blood corpuscles and less urea. Its temperature is on an average 1° C. lower (Chap. VII.) The changes effected by gases in the colour of the blood probably depend, on the one hand, on an alteration in the shape of the blood corpuscles, which shrink and become more concave in appearance on combination with oxygen, swelling out, on the other hand, on the removal of the oxygen (by the passage through it of carbonic acid, &c.) (Harless). In the first case, the blood corpuscles, acting as more powerful concave mirrors, would reflect light in a more concentrated form, whilst in the latter they would tend more to disperse it. At all events, it is in this manner that the addition of salts to the blood renders it brighter. The addition of water, on the other hand, darkens it. Gases, however, exert an action on the pigment which is quite independent of any alteration which they may bring about in the shape of the corpuscles—an action which may be observed after these bodies have been broken up by the addition of water; in lake-coloured blood, however, the colour being darker of itself, the action of oxygen is less easily seen.

The peculiar composition of particular kinds of blood (the blood of the portal, hepatic, and splenic veins), as well as the influence on the blood of digestion, respiration, etc., will form the subject of later chapters.

The changes taking place in the physical and chemical constituents of the blood, its waste and reparation, form the subject of the sixth chapter.

The Quantity of Blood in the Body.—Its Quantitative Composition.

The quantity of blood contained in the human body is not accurately known: it amounts to about $\frac{1}{13}$ (Bischoff) of the whole weight of the adult body; to about $\frac{1}{19}$ (Welcker) of its weight at birth.

The following are the best known methods for determining the quantity of the blood: 1. By ascertaining the dilution of the blood caused by the injection of a known quantity of water; the degree of dilution is determined by comparing the amount of water contained in two samples of the blood taken, the one immediately before, the other a short time after, the injection of the water (Valentin). [This gives too high a result, both because the water does not become equally mixed with the whole of the blood, and also because the

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diluted blood commences at once to diffuse throughout the tissues, giving off water (mainly through the kidneys) and taking up solid matter]. 2. By bleeding freely (by beheading) and washing out the blood still left in the vessels with water (until the latter becomes no longer coloured), the amount of the solids contained in the whole of the blood is determined; the quantity of blood can then be ascertained, by comparing these solids with the amount of solids contained in an undiluted sample of blood (Ed. Weber). [Inaccurate, both because all the blood is never washed out of the vessels, and also because the water flowing through the vessels takes up substances, by diffusion, from the parenchyma.]. 3. The blood remaining in the vessels after decapitation is diluted with water until it is identical in colour (when layers of equal thickness are compared), with a measured sample of blood previously obtained, and diluted with a known quantity of water; the quantity of blood is then easily calculated from the amount of water required for dilution (Welcker, Heidenhain). The amount of hæmoglobin contained in the muscles (Chap. VIII.) must be allowed for. It is advantageous to saturate the blood with carbonic oxide (see above), so as to avoid variations in colour, due to unequal saturation with oxygen (v. Bezold & Gscheidlen).

Note.—The following may serve as an example of the quantitative composition of the blood. Venous blood of the horse (Hoppe-Seyler) consists of 67·4 per cent. plasma, and 32·6 corpuscles. The plasma itself consists of 90·8 per cent. water, 1·0 fibrin, 7·8 albumin, 0·1 fats, 0·4 extractive matters, 0·6 soluble salts, 0·2 insoluble salts. The corpuscles contain 56·5 per cent. of water, and 43·5 per cent. solid matter; the organic constituents of the corpuscles in the human subject are (Jüdell) from 12·2–5·1 per cent. albuminoid matter, 86·8–94·3 hæmoglobin, 0·7–0·3 lecithin, 0·25 cholesterin.

Death of the Blood, and the Changes which accompany it.

So soon as blood or liquor sanguinis is withdrawn from the influence of the walls of living vessels, it quickly runs through a series of changes, which may be said to attend the death of the blood. They are as follows:

1. *Coagulation*, that is, the separation of a solid albuminous body, 'Fibrin.' The liquid blood is thus changed in the first place into a soft red mass; in a few hours, however, the solid portion contracts, pressing out a yellow fluid—the blood serum; the solid portion retains, however, the shape of the vessel containing it, but on a smaller scale. The firm red mass, the *blood clot* (placenta sanguinis), now floating in the serum, consists of matted filaments of fibrin, and the blood corpuscles imprisoned within them, together with some occluded serum. The fibrin is separated essentially from the plasma and not from the blood corpuscles; for the former, which may be obtained either by allowing the corpuscles in uncoagulated

blood to sink to the bottom, or by filtering blood containing large corpuscles (frog's blood diluted with sugared water, J. Müller), undergoes coagulation, forming a white cake which consists solely of fibrin. The serum consequently contains the same component parts as the plasma, with the exception of fibrin. If before coagulation the blood corpuscles have time to sink (as is usually the case with the blood of the horse), the upper layer of the blood clot consists solely of fibrin, without corpuscles, and is therefore white and of closer texture than the red portion ; this is called the ' Buffy Coat ' (also ' crusta phlogistica,' from its occurrence in blood obtained by bleeding animals affected with inflammatory diseases). Fibrin may also be obtained by whipping recently drawn and yet uncoagulated blood with twigs, or stirring it with a stick ; the fibrin adheres to the twigs or to the stick, in white filaments. The red uncoagulable fluid remaining—defibrinated blood—consists of the serum and corpuscles.

The process of coagulation is made plain by the following Table :

Undisturbed coagulation :	When beaten :
Blood	Blood
Plasma Corpuscles	Plasma Corpuscles
Serum Fibrin |	Fibrin Serum |
Blood clot	Defibrinated blood

The amount of fibrin is very small, in spite of the large space it takes up during coagulation, especially at first ; it is also exceedingly variable, even in different samples of the same blood (S. Mayer) ; on an average it forms about 0·2 per cent. of the blood.

It has been recently stated that even washed blood corpuscles yield fibrin (Heynsius). Embryonal blood is not at first coagulable (Boll).

2. *Acidification.*—From the time it is drawn until coagulation, the alkaline reaction of the blood steadily diminishes (Pflüger and Zuntz). This depends most probably on the formation of an acid, the nature of which is yet unknown.

3. *Deoxygenation.* — Immediately after it is drawn the amount of oxygen contained in the blood becomes somewhat diminished ; the amount of CO_2, on the other hand, being increased (Pflüger, A. Schmidt). As this consumption of oxygen takes place during life, the blood always containing oxydizable

substances (compare Chap. IV.), it probably does not properly belong to the death-phenomena, but is merely synchronous with them.

4. *Calorification.*—During coagulation a slight rise, perceptible by means of the thermometer, takes place in the temperature of the blood (Schiffer).

An evolution of electricity likewise probably takes place, under certain circumstances, during the dying of the blood. On making a cross section of fresh organs (as glands) a weak negative current is developed, as opposed to the natural surface (Matteucci). This current is, however, only apparent in organs containing blood (Hermann), and is usually absent in the organs of warm-blooded animals (Du Bois-Reymond). Most probably it arises from an evolution of electricity caused by the contact of the decomposing blood (at the incision) with the still unchanged blood in the vessels, the former becoming negative (Hermann). Since, throughout the whole ramification of vessels, the blood forms one continuous mass, the opposition between the section and the surface must depend on the difference in the speed with which the blood decomposes in each case. At the section, the blood in all cases at once dies; at the surface, owing to the protection of the tissues, it dies but slowly in cold-blooded animals, although quickly, in spite of this, in warm-blooded; thus are explained the above-mentioned facts.

The above-described phenomena show that during the process of dying the blood undergoes complex chemical changes. The most striking of these, the coagulation of fibrin, was formerly considered to be a spontaneous coagulation of an albuminous substance dissolved in the plasma. We now know that the fibrin, as such, does not exist in the blood, but originates in the process of dying. According to the ideas most generally received (A. Schmidt), it arises from the chemical combination of two albuminous substances, separate, although existing side by side, in the blood—'fibrinogen' and the 'fibrinoplastic substance.' This combination is brought about by a ferment, which is only developed during the death of blood. Both the fibrin generators are contained in the plasma.

The fibrin generators are also contained in many other normal and pathological fluids, *e.g.* in lymph and chyle, in pericardial and hydrocele fluids, &c. The former of these fluids also generate the ferment, and therefore coagulate spontaneously, although more slowly than the blood; the others do not generate the ferment, and, therefore, coagulate only after the addition of ferment or of blood. Fibrinogen and the fibrinoplastic substance are most closely related to globulin. They can be obtained from their natural solutions in blood-

plasma by the addition of water and the subsequent passage of carbonic acid; the fibrinoplastic substance is first precipitated and carries down with it, mechanically, the ferment. Both the fibrin generators are soluble in alkalies and acids and in solutions of common salt; they are soluble in water if a stream of oxygen be passed through it.

The ferment is obtained by adding alcohol to blood, and extracting the thoroughly dried and filtered residue with water. Blood allowed to flow directly from an artery into alcohol yields no ferment.

On mixing solutions of fibrinogen and the fibrinoplastic substance in the presence of the ferment, fibrin separates first as a gelatinous substance, which afterwards contracts; the quantity of the two substances determines the amount of fibrin, to form which they appear to combine, although in proportions which are not constant. The amount of ferment present merely influences the rapidity of the separation of fibrin. Serum contains an excess of fibrinoplastic substance (that of ox's blood contains 0·7–0·8, of the horse 0·3–0·6 per cent). Presence of non-crystallisable hæmoglobin, of carbon, platinum, &c. hastens the formation of fibrin, when all other conditions are present. If solutions of the fibrin generators and of the ferment are deprived of oxygen, by passing hydrogen through them, before they are mixed, no fibrin is formed (A. Schmidt).

The connection between the above and the other phenomena accompanying the death of the blood, particularly acidification, is unknown. Blood which has undergone these changes, if kept longer, particularly if defibrinated, gradually loses the whole of its oxygen, carbonic acid taking its place : at the same time putrefaction sets in.

The phenomena accompanying its death are the result of the cessation of an influence exercised constantly upon the blood during life, by the living walls of the vessels (Brücke). The blood does not coagulate as long as it circulates in the vessels, so that every portion of it constantly comes in contact with their living walls; nor does it coagulate if, after being drawn, it is in contact with a living vessel (as, for instance, when frog's blood is placed, over mercury, in contact with a pulsating frog's heart, Brücke). On the other hand, it coagulates after it has been drawn from the vessels, or in the vessels, after their death, or even in living vessels, if at any point stagnation of the blood occurs, so that the central layers are removed from the influence of the walls.

Many precise accounts concerning the causes of the process of coagulation are here passed over, because they have not been verified. According to our present views of fibrin formation, Brücke's law would be expressed as follows: the influence of the living vascular wall is to hinder the formation of the fibrin ferment, or to destroy it continuously as soon as it is formed.

All the phenomena which characterize the dying of the blood are hastened by high temperatures, and by the contact of the blood with foreign bodies (as by stirring), also by air (blood coagulates more quickly in open vessels than over mercury). Coagulation may be checked by the addition of alkalies or alkaline salts, or by precipitating the fibrinoplastic substance by means of carbonic acid or other weak acids.

II. THE CIRCULATION OF THE BLOOD.

The blood circulates continually, and with great speed, throughout all parts of the body, in the paths prescribed for it by the vascular system, which, under normal circumstances, it never leaves. All the matters given up by the blood have, therefore, to pass through the closed vascular wall, and with few exceptions (passage of lymph into the blood), this is the case with the matters absorbed into the blood. Only the thinnest portions of the vascular system, viz. the capillaries, permit of this exchange taking place.

Seeing that the vascular system is completely closed and that the movement of the blood is always in the same direction, it is clear that that movement must be of the nature of a circulation.

The vascular system may therefore be pictured as a system of continuous closed tubes, with many branches; the finest ramifications of this system correspond to the capillaries. Only in two places is the system perfectly simple; these are the aorta and the pulmonary artery, each with its appended half of the heart. From each of these places the blood can only reach the other through a capillary system: there are, therefore, two principal capillary systems, through both of which every particle of blood must pass once at each circulation—the pulmonic capillary system, and the systemic capillary system. The functional difference between these capillary systems depends on the character of the changes which the blood which they contain undergoes (see Chapter V.): in the pulmonic capillaries the blood takes up oxygen, and gives off carbonic acid; the reverse takes place in the systemic capillaries. Throughout the whole of the passage, therefore, from the pulmonic capillaries to the systemic, the blood is rich in oxygen, and consequently *bright*

red or *arterial*; on the other hand, during its passage from the systemic to the pulmonic capillaries it is poor in oxygen, but rich in carbonic acid, and therefore *dark red* or *venous.* The whole circulation, therefore, naturally divides itself into two halves, an arterial and a venous.

At the commencement of each of the trunks of the vascular system (the one the arterial, the other the venous) is placed the principal motor apparatus, in the form of two contractile pouches, supplied with valves—the two halves of the heart—the left being on the arterial side of the circulation (commencement of the aorta), the right on the venous (commencement of the pulmonary artery). Reckoning from the heart forwards, all those vessels which carry blood *to* a capillary system are called arteries, whilst those carrying the blood *from* a capillary system, are called veins. There are therefore two arterial and two venous systems. The systemic arterial system (the aortic system) carries arterial blood from the left side of the heart into the systemic capillaries; the systemic venous system carries this blood, now become venous, into the right side of the heart, from which the pulmonary arterial system carries the venous blood into the pulmonary capillaries, and the pulmonic venous system returns this blood, again become arterial, into the left side of the heart.

Although the complete circulation forms one single circuit, the course of the blood from the left side of the heart through the systemic capillaries to the right side of the heart is often erroneously described as the greater or systemic circulation, the other as the lesser or pulmonary circulation. One portion of the systemic venous blood, viz. that coming from the capillaries of the intestines and spleen, unites to form one vein (the portal vein), which does not proceed directly to the right side of the heart, but branches out, like an artery, into a second capillary system in the liver, whence it passes into veins leading direct to the heart. This section of the vascular system is erroneously called the portal circulation.

Since the sum of the diameters of the branches of an artery almost always exceeds the diameter of the trunk, the sum of the diameters of the vascular system must in general increase with its ramifications, and consequently is smallest in the two trunks (the aorta and pulmonary artery), and greatest in the capillaries. The vessels, especially the arteries, are very elastic.

Amongst the motive powers producing the circulation of the blood the movements of the heart occupy the first place.

The description of the circulation as a whole will therefore be preceded by an account of the most essential facts relating to the heart.

The Movements of the Heart.

The heart consists of two hollow muscular organs, completely divided, though of similar construction; each of these transmits its contents in a definite direction by means of rhythmical contractions and valvular arrangements. The right half of the heart is connected with the venous, the left with the arterial half of the circulation; the former therefore contains only dark red, the latter only bright red blood (p. 48);—the former transmits, through the pulmonary artery, the blood pouring into it through the venæ cavæ, the latter transmits through the aorta the blood brought back from the lungs by the pulmonary veins. Each half of the heart consists of a thin-walled antechamber (auricle, atrium), which first receives the entering blood, and a thick-walled chamber (ventricle), which forces it into the artery.

Although entirely removed from the control of the will, the muscular fibres which form the greater portion of the walls of the heart, are transversely striated; they differ however from almost all other transversely striated muscular fibres, as they ramify and join together. They form numerous layers diversely arranged—partially in spirals. Those of the ventricles spring from the fibro-cartilaginous rings at the margins of the auriculo-ventricular openings, and, in part, return to be inserted in the same, while, in part, they are inserted in the chordæ tendineæ, after forming the *musculi papillares*. The muscles of the auricles are entirely distinct from those of the ventricles, but many fibres pass from the right side of the heart to the left. This arrangement of the muscles explains why both auricles or both ventricles always contract simultaneously, whilst the movements of the auricles and ventricles are independent of each other.

The heart in mammals and birds resembles the human heart. In scaly amphibia the two ventricles communicate; in the naked amphibia only one is usually present. In the former the aorta and pulmonary artery originate from the common ventricular cavity, in the latter only one vessel leaves the ventricle, supplying blood both to the body and the lungs. In fishes and in undeveloped batrachians the heart usually corresponds to the right half only of the human heart (one ventricle and one auricle); no heart is inserted in the arterial half of the circulation, so that the branchial veins open directly into the aorta. In invertebrata, which usually possess no closed vascular system, a real heart with auricles and ventricles exists only in a few orders; in some there exists merely an open bag provided with valves (as the dorsal vessel of insects); others have no such apparatus.

The rhythmical movements of the heart consist of an alternate contraction of the auricles and ventricles. The two halves of the heart work in all respects correspondingly and simultaneously. During the contraction (systole) of the two auricles, the dilatation (diastole) of the ventricles takes place, and conversely. The systole of the ventricles directly follows that of the auricles; on the other hand, a slight pause occurs after the systole of the ventricles before the following systole of the auricles; the systole of the auricles, moreover, lasts a shorter time than that of the ventricles.

The systole of the ventricles takes up about two-fifths, their diastole about three-fifths of a complete cardiac revolution (Valentin, Landois). This, however, is only when the pulse is of normal frequency, since any change in its rate only varies the duration of the diastole, whilst that of the systole remains constant (Donders).

The heart and large vessels lie within the thorax, in a spacious, closed chamber, which, together with the lungs, they tend to fill; in doing so they are dilated beyond their natural volume (see Chapter IV.); they are, therefore, under negative pressure, *i.e.* their walls (more especially those of the auricles and of the large veins which are most yielding) are drawn apart. The relaxed heart, therefore, tends to distend itself by sucking blood out of the veins. Owing to a special contrivance, the aspiration of blood *through* the veins is not even interrupted during the contraction of the ventricle—which must be looked upon as the heart-pump proper—but proceeds continuously.

As the large veins open into the contractile auricles they possess a varying capacity. During the ventricular systole the auricles are relaxed, and are therefore in a position to receive the blood which is, in the meantime, sucked up into the thorax. During the diastole of the ventricles, on the other hand, blood flows into them from the then contracting auricles, without the passage of blood through the veins into the auricles being interrupted. The auricle must therefore not be considered as a preliminary suction- and force-pump, whose action is followed by that of a second pump, the ventricle, but is to be looked upon merely as a reservoir which regulates the pressure of blood in the venous system. Each lateral half of the heart, therefore, being a simple suction- and force-pump, merely

requires a valvular arrangement at its orifice of entrance and exit ; the first is formed by the auriculo-ventricular, the second by the semilunar valves.   During the systole of the auricles the blood is sucked into the synchronously relaxed ventricle by the aspiration of the thorax (aided, perhaps, by the active power of aspiration exerted by the ventricle in its diastole, and to which we shall afterwards refer), so that no valves are required to prevent its reflux into the venous trunks.   It is only the coronary veins which empty themselves into the right auricle, and whose contents being regulated, not by atmospheric, but by intra-thoracic pressure, require a valvular arrangement, and this is provided for by the so-called *valvula Thebesii.*

The auricular cavities are never completely obliterated during contraction, though this appears to be the case with the auricular appendages.

The action of the heart as a pump commences with the systole of the ventricles, which changes the negative pressure of the contents into a positive pressure, and causes the auriculo-ventricular valves to close.   The closure of the valves is furthered by the simultaneous contraction of the *musculi papillares*, whilst the contraction of the ventricles forces their whole contents, with great energy, into the arteries (aorta and pulmonary artery).   As soon as the systole ceases, the high pressure of the blood in the large arteries closes the semilunar valves, so that a reflux of blood into the relaxed ventricle is impossible.   After a short pause, during which, as was previously mentioned, the ventricles receive blood from the previously filled auricles, the action recommences with the auricular systole.

The auriculo-ventricular valves, viz., the tricuspid on the right and the mitral on the left side of the heart, consist respectively of three and two segments, which are connected by a broad basis to the walls of the auriculo-ventricular openings, whilst their free margins are connected to the *musculi papillares* by means of the *chordæ tendineæ*.   When not in action these valves hang slackly in the ventricles.   As soon as the pressure within the ventricle surpasses that in the auricle, the back current drives them up, causes them to unfold, and as they are prevented by the *chordæ tendineæ* from passing into the auricle, their inner borders are pressed together, so that a complete closure is effected.

The semilunar valves are formed by three pocket-like membranes situated at the commencement of the aorta and pulmonary artery.   These pouches oppose no obstacle to the passage of blood into the arteries, but so soon as the

pressure in the latter becomes greater than that in the ventricles, they fall together, and by their edges press against one another. Their edges then form a three-pointed star. In this position the semilunar valves form a strong barrier between the ventricle and artery.

The position of the semilunar valves during systole, and their relation to the coronary arteries, which take their origin in the sinuses of Valsalva, at the commencement of the aorta, are subjects of dispute. Some (Scaramuzzi, Thebesius, Brücke) suppose that during systole the valves lie close to the arterial wall, in such a manner as to close the openings of the coronary arteries, so that the latter are only supplied with blood during diastole. The result of this would be a more easy entrance of blood into the substance of the heart during its relaxation, and a distension of the ventricle in diastole, due to a turgescence of its walls, whereby an active *aspiration* of the blood streaming out of the auricle would be effected ('Selbststeuerung des Herzens' of Brücke.)

Others (Hamberger, Hyrtl, Rüdinger, Oehl, Ceradini) raise the following objections to this view. (1.) The valves are not pressed against the wall during systole, but are stretched across and away from the sinuses. (2.) When the coronary arteries are cut across, blood flows from them, specially during systole, and from their central ends too. (3.) Blood meets with less resistance in flowing through the capillaries of muscles during contraction than relaxation (compare Chapter VIII.). (4.) The capacity of the cavities of the heart is not only not increased by injection of the coronary arteries, but diminished. According to the most recent researches (Ceradini), the diastolic closure of the semilunar valves is not brought about by a regurgitation of blood, but by the elastic rebound of the aortic walls at the time when the systolic stream through the axis of the aorta is interrupted; for, during the passage of blood through the aorta, the pressure of blood at the sides of the aorta is greater than in the rapidly moving axial layers.

The shape of the relaxed heart, or more accurately, of the two ventricles, is that of an oblique cone, whose base (a section through the auricular ventricular openings) is an ellipse. By the systole of the ventricles the shape of the heart is altered in such a manner that the base becomes rounded, and the formerly oblique axis vertical, so that an upright cone is formed. The change in form is accompanied by a rotation of the axis, and, (owing to the position of the heart in the thorax,) a tilting up of its apex, which, in consequence, strikes against the wall of the chest (Ludwig). The striking of the cardiac apex against the thoracic wall may also be caused by the so-called *recoil* which is communicated in a reverse direction to every moveable body out of which a fluid is pouring (Gutbrod, Skoda). Both causes have been supposed to account for the cardiac impulse or apex beat, which may be seen and felt between the fifth and sixth left

ribs, a little to the inside of a vertical line drawn through the nipple. When the heart strikes exactly on a rib only a slight quivering is noticed.

Over the exposed heart, or when the ear is applied directly, or with a stethoscope, to the præcordial region, two sounds may be heard, following in quick succession—the heart sounds. The first (systolic) is a dull sound, loudest in the vicinity of the ventricles, and lasts as long as their systole continues. Some attribute this sound to the vibration of the tense membranous auriculo-ventricular valves, whilst others suppose it to be the *muscular noise* of the contracting heart (Chap. VIII).

That the noise of muscular contraction takes a part in the production of the first sound is known by the fact that it may be heard in a heart which has been cut out and is empty of blood (Ludwig and Dogiel).

The second, diastolic, sound follows immediately, and therefore occurs at the commencement of the ventricular diastole. It is shorter and clearer than the first sound, and is caused by the sudden closure of the semi-lunar valves, the *competence* of which is necessary to its production (Williams).

The cardiac impulse may be made to register directly the movements of the heart. For this purpose an air-tight drum is placed against the chest wall and the vibrations of the air contained in it are propagated by a suitable arrangement to a writing lever, which registers them upon a travelling band of paper (' Cardiograph ' of Marey). The arterial pulse serves for the indirect registration of the heart's action (see, below, Kymograph, Sphygmograph).

Movement of the Blood in the Vessels.

Causes.

If we imagine the vascular system filled with blood, but with every impulse to motion absent, the blood will stand everywhere within it under equal pressure, which, however, is greater than would be caused by its own weight—a proof that the volume of the blood is greater than the natural capacity of the vascular system (Brunner). If in such a system the pressure be suddenly made unequal in two places, a current will be immediately set up from the point of greater to that of less

pressure. The less the opposition to this adjustment of pressure the more rapidly does it take place, and the greater, consequently, the speed of the current. At any given moment during this process of adjustment the difference of pressure still remaining must be greater the greater the resistance. It is moreover easy to see that, other things being equal, the speed of the current will increase with the difference in pressure. A constant inequality of pressure is caused in the different portions of the vascular system by the movements of the heart, which thus produce the circulation of the blood.

Imagining the system to have been at rest, the first systole would press a certain quantity of blood (the contents of the left ventricle, see below), just removed from the venous system,[1] into the elastic arterial system, thus raising the pressure in the same. This increased pressure would immediately equalise itself, through the capillaries, with the diminished pressure in the venous system, if the blood did not meet with sensible resistance by friction[2] against the walls of the smaller vessels, particularly of the capillaries; this so delays the passage through the capillaries that the second systole follows before the adjustment is completed, causing an increased pressure in the arterial system. The same occurs at each succeeding systole, the repletion of the arterial system, and, at the same time, the pressure of the blood from the dilatation of the elastic arterial walls, thus becoming greater and greater. The increasing difference of pressure, however, tends to drive the blood more and more quickly through the capillaries, and it becomes at last so

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[1] For the purposes of the following explanation, the right auricle is considered as opening into the left ventricle, the pulmonary circulation, including the right ventricle and left auricle, being left out of the question.

[2] The resistance to a fluid running through a tube, provided that, like water or blood, it adheres to (wets) the wall, is not caused by the friction against the wall, but by the so-called 'internal friction.' The outer layer of such a fluid remains entirely without motion. If we imagine the whole mass to consist of very thin concentric layers, that layer which is next to the immovable one must rub against it, and so the others, each against the one immediately outside. Every such contact causes resistance by friction ('internal friction'), and thus consumes a portion of the motive power—that is, converts it into heat; each layer is consequently delayed in its course, and the outer ones must naturally be the most delayed, the inner, therefore, the least: consequently the speed is greatest at the axis. It follows that the delay of the axial layer will be greater in narrow than in wide tubes.

great that as much blood is pressed through the capillaries during the period between two systoles as each systole pours into the arterial system. Under these circumstances no increase of pressure can take place; the difference in pressure now existing between the arterial and venous systems is a *constant* one; it causes a continuous stream through the capillaries, carrying through them just so much blood as the heart rhythmically empties into the arteries. The rhythmic transfer from the venous into the arterial system is thus converted into a continuous current from the arterial into the venous system, through the capillaries (E. H. Weber).

The contents of the left ventricle, that is, the quantity of blood pumped out during one systole has been calculated variously at from 150 to 190 grammes. The following are the principal methods: 1. (Legallois, Colin.) The content of the ventricle may be directly measured by filling the ventricle, before rigor mortis sets in, with a fluid of known specific gravity, and weighing before and after: in this case, as it is impossible to imitate the normal pressure of the heart, the result is valueless. 2. (Volkmann.) The diameter of the aorta, and the speed of the current of blood within it, are used to calculate how high a column of blood the heart expels during a unit of time; knowing the frequency of the pulse, the quantity emptied during each systole is found to be about $\frac{1}{400}$ of the weight of the body; that is, in a body weighing 75 kgrms. = 187·5 grms. 3. (Vierordt.) Given the speed of the blood in any section of the arterial system, the area of that section, and also the area of the aorta, the mean speed in the latter can be calculated, and also the quantity of blood discharged from the left ventricle during a unit of time, since the speed in any two sections is in inverse relation to their contents. The quantity of blood which the right ventricle drives into the pulmonary arterial system must be very nearly the same as that expelled by the left, because the same quantity of blood flows through every section of the vascular system during the same time (see below), and both sides of the heart contract synchronously.

The distension of the arteries and the slackness of the veins show in the simplest manner how much higher is the tension (blood pressure) in the arterial than in the venous system; this is also shown by the height of the jet of blood issuing from an open vessel; from a vein this is seldom of a notable height, whilst the blood from an artery, on the other hand, spurts to the height of several feet.

Absolute determinations of the pressure of the blood may be made by connecting the vessel, laterally, with a manometer: or the blood itself may be employed as the manometric fluid,

by letting it rise in a vertical tube, and measuring the height of the column (Hales). It is much more advantageous, however, to use the mercurial manometer (Poiseuille) as an ' hæmatodynamometer,' placing a solution of sodium bicarbonate between the blood and the mercury to prevent coagulation. *A priori*, it follows that the blood pressure (that is, the *mean pressure*, apart from the fluctuations of the pulse wave) at one and the same spot of the arterial system will increase: 1. With the fulness of the vascular system, that is, with the quantity of blood. 2. With the frequency and force of the contractions of the heart, for the greater the quantity of blood pumped by the heart from the veins into the arteries, the greater—as is shown above—will be the constant difference in tension between the venous and the arterial systems. The tension, moreover, must vary in different parts of the arterial system. Since any opposition hinders the equalising of the difference in tension, the resistance offered in any one portion of artery by the friction against its walls has an influence on the tension of that particular portion of the arterial system, similar to that of the capillaries on the general tension of the arterial and venous systems. The tension must always be greater before any point of opposition than behind. It follows, therefore, that the blood pressure in the arterial system gradually diminishes from the left ventricle to the capillaries ; that the diminution is most rapid where there is the greatest resistance, that is, where contractions occur and where branches are given off from the trunk, especially if at considerable angles ; and that, lastly, the pressure in the principal arterial trunks, on account of their size and the small number of their branches, remains very nearly identical with that of the bulbus aortæ, whilst it diminishes in the smaller arteries (H. Jacobson). Finally, on account of the less resistance offered by the capillaries of the lungs as compared with the capillaries of the body, the difference in tension between the pulmonary arteries and veins will be less, and the pressure in the pulmonary arteries will therefore also be less, than in the systemic arteries, since the quantity of blood rhythmically pumped over is the same in each. In the human aorta the blood pressure has been estimated at 250^{mm} Hg. ; in the brachial artery it has been directly determined at from 110–120^{mm}

(Faivre). In the pulmonary artery it is said to be about one-third as high as in the larger systemic arteries (Beutner).

The work done by the right ventricle (*i.e.* the product of the mass of blood raised into the height to which it is raised) is (three times) less, and its muscular coat therefore thinner, than that of the left. The work of one systole of the latter, reckoning the quantity of blood at 175 grms., and the aortic pressure at 250ᵐᵐ Hg. (= 3 mtr. of blood) may be reckoned at 0·525 of a kilogrammetre, and the work of twenty-four hours (seventy-five systoles in the minute) at 56,700 kilogrammetres. The work of the whole heart, therefore, amounts to about 75,600 kilogrammetres. Since therefore the weight of the heart is 292 grms., it would raise its own weight 10,788 mtrs. in one hour. As already shown, the whole of this work is converted into heat, by friction in the vessels. Concerning the means which exist for preserving a constant pressure of blood see below.

The continuous stream of blood through the capillaries presupposes an almost constant tension of the arteries leading immediately into them, so that in these the increase of pressure corresponding to the systole can be scarcely appreciable. Following the arterial system, however, backwards to the heart, we find in every portion of it a regular fluctuation in pressure, that is, an increase of pressure corresponding to the systole, and a diminution answering to the diastole. This fluctuation of pressure, which can be easily demonstrated in any artery, is the more considerable the nearer it is to the heart, and therefore, is greatest at the commencement of the aorta (and pulmonary artery), and least, almost unnoticeable, in the terminal arteries; this fluctuation of pressure is called the *pulse*. It does not occur synchronously throughout the whole arterial system, but each phase of it (for instance, its maximum) shows itself first nearest the heart; that is, the fluctuation in pressure travels, in the form of a *wave*, from the heart to the capillaries through the arteries, losing constantly in intensity. For the blood, pressed during systole into the commencement of the arterial system, at first increases the tension in that part alone; the next moment, however, this portion of artery, distended beyond its diastolic volume, tends to relieve itself of its excess by its elasticity: the return of the blood is prevented by the closure of the semilunar valves; the surplus is therefore forced forwards, and, as in any elastic tube, the distension travels on towards the capillaries. If the arterial system ended in closed tubes, it is plain that the wave would run to the end in undiminished size,

and be then reflected back again. But since the continual drain through the capillaries constantly diminishes the systolic excess in the arterial system, so that, according to Weber's theory, it entirely disappears before the following systole, the wave, during its course, becomes gradually smaller, until, at the end of its journey, it disappears. In certain cases, however, the pulse wave passes into the capillaries, and, through these, even into the veins ; that is, in other words, in certain cases the plan described above is not carried out perfectly : the stream through the capillaries becomes no longer continuous, but the cardiac rhythm rules even in them :—this takes place when the resistance of an artery is diminished by its sudden enlargement, so that the balance hitherto existing between the resistance and the difference in tension of the arterial and venous systems becomes locally disturbed, as, for instance, by the division of the *vaso-motor* nerves (Bernard).

The speed of transmission of the pulse wave (not to be confounded with the speed of the blood current, to be afterwards considered) may be measured with a watch, by comparing the moment of passage of the wave in a distant artery with the moment of systole, or with the moment of the pulse in an artery near the heart. On an average, it travels 28·5 feet per second (E. H. Weber).

In investigating the pulse, both the rise in the pressure of the blood and the increase in size (perceptible to both sight and touch), which take place in every artery during the passage of the pulse wave, are made use of. The former causes regular movements of the mercury in a manometer connected laterally with an artery. In order to show these plainly, a float is placed on the mercury in the open limb, and this, by means of a brush, traces them on a drum, regularly rotating (by clock-work) on a vertical axis (Ludwig's Kymographion). The up and down movements of the mercury then form wave-like curves. These, however, give no exact indication of the actual extent of the fluctuations in pressure, because the mercury, on account of its inertia, soon sets up oscillations of its own, which, although of the same duration as the pressure fluctuations, do not run the same course. In order to ascertain the course of the fluctuation in pressure, other manometers are used ; for instance, a bent elastic tube filled with fluid, which is expanded by pressure on its contents (Bourdon's manometer, Fick's kymographion) ; or an elastic bag filled with fluid, and placed in a closed tube containing air, its changes in volume being transmitted by the air (Marey's kymograph) ; or the dilatation of the artery is used directly, and for this sphygmographs are employed. These instruments are applicable even to the human subject ; over the artery is placed a small plate, which, following its dilatation and

contraction, moves a sensitive lever: the latter is made to write either on a rotating drum (Vierordt), or on a travelling tablet (Marey). The best results are given by Marey's instrument, because in it the oscillations originating in the lever itself are prevented, as far as possible, by diminishing its size, and counteracted, as far as practicable, by means of springs.

Under normal conditions the pulse in most arteries has a double (dicrotic) or even triple (tricrotic) beat. The second and third beats, however, can only be observed with fine instruments (with Marey's sphygmograph for instance) as small eminences on the descending portion of the pulse wave (Marey, Wolff, Rive). They are caused partly by the reflection of the wave from the end of the artery, partly by the back current on the closing of the aortic valves. For the respiratory fluctuations of pressure in the arteries see p. 67, for an active motive power of the same see p. 68.

The pressure of the blood in the capillaries cannot be measured; its changes, however, can be estimated from their size and from the amount of fluid which filters through them (Chapter II.). According to the scheme of the circulation previously described it must be constant, except when, as in the above-cited cases, the pulse wave is transmitted to the capillaries. Any diminution in the resistance of the vessels leading from the capillaries will increase it. It rises and falls, moreover, with the general pressure of the blood.

In the veins the blood pressure, appreciable with a mano-meter, is extremely low, being slightly negative in the large venous trunks, and increasing towards the periphery. Just as each rhythmic injection of blood into the arteries produces a rising wave in them, so each rhythmic removal of blood from the venous system would cause a falling wave passing from the capillaries, if this were not prevented by the auricles.

There are two other circumstances of such importance in the circulation of the blood, that they may be classed along with the contraction of the heart as causes of the circulation: they are the aspiration of the thorax, and the adventitious compression of the veins.

The Aspiration of the Thorax.—Owing to their position in a large cavity, which they (together with the lungs) must assist in filling, the heart and the large vascular trunks are dilated beyond their natural volume, and are consequently more completely filled with blood than they would be under other circumstances. This especially affects the more yielding portions — that is, the venous trunks and the auricles. As already mentioned when speaking of the heart, the aspira-

tion of the thorax causes the blood, flowing through the venous trunks opening into the heart, to be immediately replaced by the flowing in of fresh blood from veins situated outside the thorax, and this essentially aids the circulation. Each inspiration, by its consequent enlargement of the cavity of the chest, further increases the negative pressure, and thereby causes over the whole mass of blood an aspiration in the direction of the thorax ; but this aspiration will mainly affect the venous system. In the arteries it causes merely a slight decrease of tension ; *on the other hand, it draws the venous blood powerfully towards the heart.* An *ordinary* expiration merely removes the inspiratory increase of the negative pressure ; on the other hand, a *powerful* expiration, caused by muscular exertion, especially if an obstacle be opposed to the exit of the air by closure of the glottis (as in coughing), changes the negative pressure in the thorax into a positive one, compressing the heart and vessels (in particular the veins), and causes in the veins a serious stagnation, and in the arteries a less important increase in pressure. In consequence of this, the central end of a divided vein sucks in air during inspiration, and this may lead to fatal consequences by leading to embolism of the pulmonary capillaries : on the other hand, the veins swell considerably during a powerful expiration, particularly during coughing. If after a deep inspiration the glottis is closed, and a powerful attempt made at expiration, the positive pressure in the thorax becomes so great, that the venous trunks are almost closed, less and less blood pours into the heart, and at last the circulation is entirely stopped (E. Weber). The action of these thoracic conditions on the arteries shows itself likewise in a regular fluctuation of the blood pressure (increase during expiration, decrease during inspiration), which is synchronous with the movements, not of the heart, but of breathing, and is therefore four times as slow as the pulse.

On account of this the pulse waves of the kymographion curve appear to be made up of a second (respiratory) system. If, by interposing a narrow tube between the artery and the manometer, the pulse waves be prevented from affecting the manometer, the respiratory waves are obtained alone (Setchenow).

Transient, adventitious, compression of the veins by the contraction of neighbouring muscles.—Any such compression of a

portion of a vein must press its contents *in a direction towards the heart,* since the passage in the opposite direction is stopped by the self-closing venous valves. This compressing apparatus is in some places joined to an aspirating arrangement; thus the portion of the femoral vein lying under Poupart's ligament sucks in the blood from the periphery at each turn in an outward direction of the upper part of the thigh, and empties it into the vena cava on each turn in an inward direction, or on flexion (Braune).

The movement of the blood in the veins consequently is as follows : when the blood has flowed through the capillary system, its speed, according to the above scheme, almost $= 0$, because the tension in the arterial system is only sufficient to drive the necessary amount of blood (about 175 grms. in $\frac{1}{75}$ minute) through the capillaries. The force of the heart therefore, being entirely expended in overcoming this resistance, (being converted into heat,) has no influence on the flow of blood in the veins.[1] On the other hand the following forces come into action : 1. Gravity : this can only aid the circulation in the descending veins (as, *e.g.,* those of the head when upright), while on the other hand it checks it in ascending veins : the veins of the foot for instance, under the pressure of their high column of blood, would be so enormously dilated and stretched, and the resistance caused would be so great, that the whole movement of the blood in the lower extremities would be stopped. The other forces, therefore, which co-operate in the maintenance of the venous circulation are of the greatest importance, viz. 2. *The aspiration of the thorax,* particularly *during inspiration,* and 3. *The muscular movements of the body.* From what has been stated it follows that the venous circulation goes on very irregularly.

The movement of the blood in the *capillaries,* which may be observed under the microscope in transparent parts (for instance in the web and mesentery of the frog, in the omentum

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[1] This does not hold good in its entirety : the real conditions are more complicated than the theoretical (Weber's) statement given here, for in many cases the local tension of the artery exceeds this limit, and the blood enters the veins with perceptible velocity, frequently under such pressure that, if cut, the veins spurt. We therefore usually find included amongst the forces causing the venous flow 'the residue' of the motive power of the arterial system (' vis-a-tergo, vis inertiæ,' &c.).

of the guinea-pig,—in the latter case on a hot stage, Stricker), frequently changes its direction in the branchings of their fine network. At the same time the movements of the blood corpuscles give one the opportunity of observing the unequal speed of the different layers of blood previously alluded to; those floating in the axis having the greatest, those next to the walls a far lower, rate of speed. In the finest capillaries, through which only one row of red blood corpuscles can force themselves at a time, the latter may frequently be seen to accommodate their shape to their surroundings,—they become lengthened, bent, and curved, and pressed together until all shape is lost, and then again assume their natural form. For the emigration of the blood corpuscles, see the Appendix to this Chapter.

Velocity of the Circulation.

If a fluid be circulating through a system of tubes, the same quantity of fluid must flow through any collective cross-section of the system during a given time. Whenever, on account of some obstacle, this condition is not fulfilled, if the system is dilatable, the section must become proportionately enlarged in front of the obstacle, and a repletion of vessels takes place. Thus for example the resistance of the capillaries causes the constant repletion of the arterial system. If, however, the circulation is in undisturbed progress, the *same quantity of blood must flow through any collective cross section of the vascular system during a unit of time.* It follows, moreover, from this, that *the speed of the current* in the various collective cross sections is *inversely proportional to the area of the cross section:* it is, therefore, greatest in the commencement of the aorta and the pulmonary artery, least (about 400 times less than in the aorta) in the capillaries. Similar conditions control the speed in the total cross sections of a single branched or unbranched vascular segment: thus, the blood flows at the same speed throughout the whole length of an unbranched vessel of uniform size.

But the quantity of blood which flows through any cross section of the vascular system during a unit of time, naturally depends on the number and strength of the contractions of the

heart.   Let n be the number of systoles during the unit of time, a the amount of blood contained in a ventricle; then the amount of blood m flowing in a unit of time through each section is represented by $m = n\,a$, that is, in the human subject about 218 grms. per second.

The rate of flow through the individual vessels, which make up a collective section of the system, will, it is clear, depend principally on the resistance which they offer, for the speed will be the less, the greater the resistance, *e.g.* in narrow vessels, which give off branches at large angles.   That the speed moreover varies greatly in the different layers of a vessel has been already shown.

Regular fluctuations of speed only take place when the plan of a continuous stream is not perfectly carried out, as is the case in arteries, through the influence of the pulse wave, and similarly in the capillaries and veins when the pulse wave, as will exceptionally occur, reaches them (p. 65).   That the passage of the pulse wave must cause a momentary acceleration in each portion of the artery, follows from what has been before stated, for the wave crest increases tension at a particular place, while the tension is still of the diastolic height in neighbouring parts, and the speed increases with the difference in tension. In the capillaries and veins, leaving out of the question the cases of exceptional presence of pulse, the speed would be constant, were it not that, in the latter, there are many influences at work producing great irregularities.   The stream of blood through a vein may frequently be completely stopped; this may, however, be unproductive of harm, since most sets of capillaries have several efferent veins, so that if the stream of blood is obstructed or arrested in one, the blood flows more quickly through the others.

The following methods are employed to measure the speed of the current in the arteries:—1. Volkmann's hæmodromometer is a glass tube of known volume, filled with water, which can suddenly be inserted into the stream of the artery.   The time that the blood takes to run through the tube and displace all the water is measured with a watch.   A modification of this is Ludwig's 'Stromuhr;' it consists of two (spherical) dromometers, which are alternately filled, the fluid (oil) being driven each time from one to the other.   2. The tachometer (employed by Vierordt) is a tube inserted in the artery; the tube contains a light pendulum. The movements, which may be observed externally, stand in a previously determined relation to the

velocity of the stream, which acts on the pendulum.   If the latter is joined
to a sensitive lever, outside the tube, curves may be obtained, whose ordi-
nates will give the speed of the current ('dromograph,' Chauveau and Lortet).
3. The determination of the amount of blood flowing from an open artery, the
tension being maintained pretty constant by regulating the size of the open-
ing (Vierordt).   Such determinations have naturally not been made in the
human subject.   (In the carotid of dogs the speed varies from 200 to 700^{mm}
per second).   In animals the speed in the capillaries is determined by direct
microscopic measurement of the course a blood corpuscle runs over in a given
time (E. H. Weber); in the human subject, by personal observation of the
entoptic visible movements of the blood corpuscles in the vessels of the retina
(Ludwig); by the latter method Vierordt found them in himself $=0.6-0.9^{mm}$
in a second (compare Chap. X.)   The speed in the veins may be measured
with the 'Stromuhr' (Cyon & Steinmann).

In order to measure the time in which a portion of blood travels through
a given portion of the vascular system, or indeed through the whole round
of the circulation, an easily recognisable salt (ferrocyanide of potassium) is
injected into the central (cardiac) end of a vein, and the time noted at which
it is detected (by chloride of iron), in samples of blood taken at short
intervals from the peripheral end of the same vein (Hering).   The first
discovered traces of the salt must have traversed the right side of the heart,
the capillaries of the lungs, the left side of the heart, and the capillary terri-
tory corresponding to the vein which is experimented upon, before reaching
the place where they are found.   According to such experiments a complete
circulation occupies 15·2 seconds in dogs, and about 23 seconds in the human
subject.

Distribution of the Blood in the Body.

*The quantity of blood contained in any portion of the body
in a given time depends :* 1. On the number and size of the
afferent arteries. 2. On the speed of the current within them.
The latter, as stated above, depends on many circumstances,
particularly on their greater or less distance from the heart,
on the number and angles of their branches, &c.   For the
changes in the size of an artery, see below under 'Innervation
of Vessels,' where further particulars will also be found concern-
ing the distribution of the blood in the body.

The distribution of blood in the individual parts of the body
may be determined in the dead subject by the same methods as
serve to ascertain the total amount of blood in the whole body
(p. 49).   The individual parts of the body to be experimented
upon must, of course, be separated when they are in a frozen state
(v. Bezold and Gscheidlen).

Influence of the Nervous System on the Circulation of the Blood.[1]

The nervous system has a direct influence on the movements of the blood, 1, by its control of the movements of the heart; 2, by its control of the calibre of the vessels, particularly of the smaller arteries, for the latter are supplied with muscles, on whose state of contraction their size depends. Not only is the supply of blood to individual organs regulated by changes in the capacity of a vessel, but change in the capacity of a large number of arteries, and the consequent change in the contents of the whole arterial vascular system, has a great influence on the activity of the heart.

1. Innervation of the Heart.

a. Intracardiac Centres.

The heart, removed from the body, or separated from all the nerves supplied to it, still beats for some time; in cold-blooded animals for days, in warm-blooded animals so long as a supply of oxygenized blood is provided. Its movements must, therefore, at least in part, be caused by a mechanism situated within itself, and the latter is supposed, with the greatest probability, to reside in the ganglionic cells (connected together by nerve fibres), which are lodged in the muscular substance of the heart, particularly in the septum between the auricles, and at the junction of the auricles and ventricles (Remak). At least a portion of these ganglia must cause the *automatic* rhythmical contractions of the heart, and indeed the whole process of contraction (from the auricles to the ventricles) must be regulated and combined by them. In a heart which is at rest, but still excitable, one or more regular contractions of its various divisions may be produced, by reflex action, on applying different stimuli (mechanical, thermal, chemical, or electrical) to the substance of the heart: greater effect is obtained by stimulation of the inner than of the outer surface of the heart.

[1] It is advantageous to refer to the influence of the nerves when considering the principal processes of molecular change, although by such anticipation many ideas are introduced, which are only explained in the Third Part of this work.

Portions of the muscular substance of the heart which contain no ganglia may, like all other portions of muscles, be thrown into simple contraction by direct irritation.

In the frog's heart the principal ganglionic masses (Remak's ganglia) lie in the wall of the sinus venosus. After the separation of the latter, the heart ceases to contract, whilst the sinus itself continues to pulsate (Stannius). Other injuries which merely affect the sinus cause the heart to stand still (v. Bezold). A second ganglion (Bidder's ganglion) lies near the junction of the auricles with the ventricle; if the heart which has been separated from the sinus venosus, and which is not pulsating, be divided in this region, that portion again commences to pulsate rhythmically in which the ganglion has been left; usually the ventricles, sometimes the auricles, or both auricles and ventricles. These pulsations are, however, temporary, and appear to depend upon mechanical irritation of Bidder's ganglion, which usually is not in a state of activity. (Even when this separation of auricles and ventricles is not effected, the heart which has been separated from the sinus, and which is motionless, may be made to pulsate for a time by a puncture into the line of junction of auricles and ventricles, H. Munk). Some attribute the arrest of the heart which follows its separation from the sinus venosus, to irritation, caused by the section of the fibres of the vagus (Heidenhain). The hypothesis that inhibitory centres exist which have their seat in the auricles, and which are unable to control the combined motor powers of the sinus and the ventricle, whilst they can control the latter by itself, although capable of accounting for the phenomena to which reference has been made, is unnecessary.

b. Inhibitory Nerves.

Even the nerves which enter the heart from the cardiac plexuses, and which are derived partly from the pneumogastric, partly from the sympathetic, exert an influence upon the movements of the heart. The fibres contained in the vagus possess the power, when they are continuously irritated by mechanical, chemical, or electric means, of *slowing*, or weakening (Ludwig and Coats) the contractions of the heart, and when subjected to a more powerful irritation, of bringing the whole heart to a stand-still in diastole (Ed. Weber, Budge). In mammalia, and especially in man, such an excitation, originating in the origin of the vagus in the medulla oblongata, is kept up throughout the whole of life, so that section of the vagi suddenly increases the frequency of the pulse.

The vagus contains, in addition to inhibitory fibres, others which accelerate the heart. Very slight excitations of the vagus occasionally cause an increase in the number of heart-beats (Schiff, Giannuzzi).

In relation to the heart, the vagus belongs to the group of '*regulating nerves*' (consult on this subject Chapters IX. and XI.).

In man the vagus can be occasionally irritated by mechanical means, as by pressure (Czermak, Concato).

When both vagi are subjected to the same degree of irritation, it is found that the right vagus possesses, in the lower animals, a more powerful inhibitory action on the heart than the left (Masoin, Arloin, and Tripier). A short interval elapses between the time of commencement of the irritation of the vagus and that of the display of its inhibitory action ('Latent period,' Donders and Prahl). The irritation of the vagus need not necessarily be the same as that required to induce tetanus generally, in order to induce the inhibitory influence, but it suffices if it consists of separate irritations following one another rhythmically with moderate rapidity (v. Bezold). During the arrest of the heart brought about by irritation of the vagus, any immediate excitation of the organ gives rise to a single and regular contraction.

In the heart of the frog, the phenomena due to irritation of the vagi may be induced by exciting the *sinus renosus*, to which the fibres of the vagus run. Poisoning with curare, as well as powerful cooling, paralyses the terminations of the vagus in the heart.

c. *Accelerating Nerves.*

Irritation of the medulla oblongata causes an acceleration of the heart, provided that the communication with the heart through the spinal cord, the *rami communicantes* which proceed from it to the sympathetic cord, the first thoracic ganglion (*ganglion stellatum*), and the sympathetic cord itself, be all uninjured.

This acceleration is a complex phenomenon, inasmuch as excitation of the medulla oblongata produces simultaneously a contraction of the arterial system, which increases the frequency of the pulse (Ludwig and Thiry). As, however, the quickening of the pulse occurs even when the influence of the vaso-motor nerves is withdrawn (by division of the chief vaso-motor nerves, as, *e.g.*, the splanchnic nerves), and as this quickening occurs more rapidly when the nerves going to the heart are preserved than when their influence is removed (in which case increase in the frequency of the pulse could only be brought about indirectly), we must conclude that there does exist a system of fibres which accelerate the heart's action, and which pass to the heart through the above-mentioned channels. The centre whence these fibres proceed appears to

exist in the medulla oblongata. This centre is not continuously in action, seeing that after division of the splanchnics section of the spinal cord induces no diminution in the number of heart beats (the brothers Cyon). According to some authors (Schiff), the vagus contains, in addition to the *inhibitory*, also *accelerator* fibres. Schmiedeberg has proved this to be the case in the frog.

As the great majority of the *vaso-motor* nerves leave the spinal cord below the second dorsal vertebra, whilst the accelerating nerves of the heart are given off above, and as irritation of the cervical portion of the spinal cord, after section at that vertebra, induces quickening of the heart without any increase in the blood pressure, a further proof is afforded of the existence of accelerating nerves (v. Bezold). The accelerating nerves belong to the group of regulating nerves.

2. Innervation of Blood Vessels.

The calibre of the arteries varies, quite independently of their elasticity, with the degree of contraction of the smooth muscular fibres which are contained in their coats. The latter are influenced by a variety of circumstances; thus, contraction of arteries is increased by cold, and diminished by heat. Even the blood pressure and the quantity of gases which the circulating blood contains appear to exert an influence on the contraction of arteries (Ludwig and Sadler, Ludwig and Hafiz); chiefly, however, the calibre of the arteries depends upon the state of irritation of the nerves which govern the muscular structures of the vessels, the *vaso-motor nerves* (Bernard). In the case of the majority of these a continuous ' *tonic* ' state of excitation has been proved to exist, so that their section leads to a paralysis of the muscular fibres of vessels, to a dilatation of the artery, to an increased flow of blood through the organ concerned, and, consequently, to its becoming red, to its temperature becoming higher, and to an increased transudation through its capillaries. The flow of blood may, under these circumstances, increase so much, that the blood may pass into the veins without having lost its arterial colour, and the pulse waves may be propagated even to the veins (Bernard). The irritation of the peripheral end of vaso-motor nerves must, conversely, lead to a narrowing of arteries, and to a diminution of the flow of blood, even to its complete stoppage, so that the

parts of the body concerned necessarily become pale, cold, and the seat of scantier transudation from the blood.

A *peristaltic contraction* of the arteries, passing *from* the main trunks *towards* the capillaries, would drive the blood actively into the capillaries, and thus aid in the circulation. That this takes place during life is not positive. After destruction of the motor power of the heart, however, an active emptying of the arteries into the veins is brought about by stimulation of the vaso-motor centres, (Goltz, Thiry, v. Bezold,) and it is probable that the emptiness of the arteries after death is to be attributed to the persistent activity of the same centre.

Blushing and erection of the penis are the best known phenomena produced by the action of nerves on the local movements of the blood. The vaso-motor nerves run partly in spinal, partly in sympathetic trunks; for instance, in the cervical portion of the sympathetic for the scalp, conjunctiva and salivary glands (Bernard); in the anterior roots of the spinal nerves for the lower extremities (Pflüger), first, however, joining the rami communicantes of the sympathetic (Bernard). The vaso-motor nerves of the upper extremities proceed from the middle dorsal roots to the sympathetic chain, thence to the first thoracic ganglion, and thence through the rami communicantes to the plexus brachialis (F. Cyon). The capacious vascular system of the viscera [1] receives its fibres from the splanchnics, which are, consequently, the most influential of the vaso-motor nerves (v. Bezold, Cyon and Ludwig). Vascular nerves, possessing direct *powers of dilatation,* are also asserted to exist (Bernard, Schiff), but whether the surmise is correct has not yet been decided; at all events, their action is as yet obscure. Stimulation of the nervi erigentes causes relaxation of the arteries of the penis (Lovén); the same effect is produced in the salivary glands (compare Chapter II.) by stimulating the cerebro-spinal fibres (Bernard). By stimulation of the spinal cord, the muscular arteries are not contracted, like others, but enlarged (Ludwig and Hafiz). For reflex enlargement of the arteries see below.

A common *central organ* for the vaso-motor nerves is situated in the medulla oblongata, by stimulating which, the spinal cord and sympathetic being uninjured, contraction of all the small arteries is produced, and, as a consequence, increase of the blood pressure in the arterial trunks, and turgescence of the heart (Ludwig and Thiry); for a description of this see Chapter XI. This central organ is constantly in action, and this explains the *tone* of the vaso-motor nerves. Division of the spinal cord in its cervical portion abolishes this

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[1] This vascular division is so large, that it can contain almost the whole of the blood of the body: on tying the portal vein, for instance, animals subjected to the operation die of anæmia, because the whole of the blood remains in the visceral vessels (Ludwig and Thiry).

tone, thus causing dilatation of all the arteries. Numerous researches, particularly on inflamed tissues, as well as those previously referred to on the direct influence of temperature, point to the existence of ganglia, in the vicinity of vessels, the function of which is to rule over their calibre.

3. Origin of the Excitation of the Nerve Centres which preside over the Heart and Blood Vessels.

The cause of the continuous rhythmical contraction of the intracardiac nerve centres is wholly unknown to us. We, however, know that the presence of oxygen (Ludwig, Volkmann, Goltz) and a temperature not far removed from that of the animal's blood are necessary conditions of its occurrence. A rise of the blood pressure within the heart (induced, for instance, by tying the aorta, or by causing the smaller arteries to contract by irritating either the vaso-motor centre, or the more important vaso-motor nerves themselves, as the splanchnic) leads to a quickening of the heart beats, which is probably due to a direct irritation of the powerfully distended cardiac walls. Conversely, when the blood pressure falls (as when the spinal cord or the splanchnic nerves are divided) there is a slowing of the heart (Ludwig and Thiry).

The increased frequency of the heart's action, which has been referred to, and which is occasioned by a rise in the blood pressure, appears so to augment the amount of work performed by the heart as more than to compensate for the increased resistance which it has to overcome ; for in warm-blooded animals when the smaller arteries are made to contract (by irritation of the medulla oblongata, &c.), the velocity of the blood current through the arterial branches increases (Heidenhain).

Temperatures from 4° C. to 0° C., and above 30°–40°, arrest the contraction of the heart of the frog (Schelske, E. Cyon). The frequency of the heart beats increases with rise in temperature until the superior limit is nearly reached. The intensity and steadiness of the contractions is greatest at low or medium temperatures. Between 30° C. and 40° C. they diminish. The sudden action of high temperatures leads to the same effects as irritation of the vagus. If, however, the heart has been previously strongly cooled, rapidly succeeding beats, and ultimately tetanus of the heart, follow the application of heat. When the heart has ceased to beat in consequence of a high temperature, irritation of the sinus venosus (which previously leads to stoppage of the heart through irritation of the vagus) causes a tetanic contraction of the ventricle (E. Cyon). Even in warm-blooded

animals the frequency of the pulse increases, in general, with the temperature of the body.

Tetanising currents acting upon the heart abolish the rhythmical activity of its nerve centres, and occasion merely ineffectual spasmodic movements, which are accompanied by a marked fall in the blood pressure (S. Mayer). The same action is exerted by strong constant currents. Weak constant currents conducted from the base of the heart to its apex occasion rhythmical contractions in the heart which has been separated from its *sinus*. With a reversed direction of the current, the contractions commence in an abnormal manner in the ventricle (Bernstein), a phenomenon which has not yet received a satisfactory interpretation.

The Inhibitory Centre in the medulla oblongata, which appears to be constantly in action (*i.e.* excited) in warm-blooded animals, like the respiratory centre in its vicinity, is under the influence of numerous centripetal nerves, whose irritation slows the heart, so long as the vagus is uninjured. To this class of nerves belong the different sensory nerves (Lovén, Kratschmer), the vagus itself (v. Bezold, Donders, Aubert and Roever; one vagus being excited whilst the other is intact), the cervical and abdominal cords of the sympathetic, and the splanchnic (Bernstein); mechanical irritation (by blows) of the abdominal viscera similarly slows the pulse by acting in a reflex manner on the vagi (Goltz). Conversely, the excitation of the inhibitory centre is diminished by inflation of the lungs (Hering). In addition, the excitation of this centre is increased, like that of respiration, by an asphyxiated state of the blood; it may, indeed, under these circumstances, assume a rhythmical action similar to that of the respiratory centre (this occurs when the lungs are filled with air containing much carbonic acid); even under normal circumstances there appears to be an increased excitation of the vagus centre corresponding to each inspiration (Donders).

A rise in the arterial pressure in the brain increases the activity of the inhibitory centre.

Division of the above-mentioned sympathetic nerves is said to diminish the tonic excitation of the vagus, which must therefore only be of a reflex nature (Bernstein).

The reflex actions likewise referred to in the preceding paragraph, like many others, are prevented by the powerful irritation of sensory nerves.

Nothing is known concerning the circumstances which influence the activity of the centre of the *accelerating nerves.*

The activity of the vaso-motor centre depends upon conditions which are very similar to those which affect the inhibitory centre for the heart. Centripetal nerve fibres which intensify the tonic excitation of the centre (so-called '*pressor*' fibres) are contained in the vagus, specially in its superior laryngeal branch, and even more abundantly in the cervical sympathetic (Aubert and Roever); further, every excitation of a sensory nerve leads to a general contraction of blood vessels (Lovén).

Certain centripetal (*depressor*) fibres contained in the vagus, which in some animals are contained in a separate branch which arises from the heart, the *ramus depressor* (Cyon and Ludwig), *diminish* the vascular tone.

The centripetal irritation of many sensory nerves causes dilation of the vessels distributed to the part supplied by the nerve (Lovén).

The *tone* of the vaso-motor centre is, further, dependent upon the gases contained in the blood. When the quantity of carbonic acid increases (in asphyxia, when an atmosphere containing much carbonic acid is inhaled) the smaller arteries generally contract with an increase of the intracardiac pressure and a distension of the heart (Thiry); this contraction intermits, however, in a regular rhythmical manner (Traube) and the rhythm coincides with the respiratory excitations (Hering). These phenomena occur even when the carotids have been occluded, whereby the blood which is stagnant in the brain becomes fitted to induce dyspnœa (Nawalichin; compare Chap. IV.).

The inhalation of irritating vapours through the nostrils exerts a *pressor-influence* through the medium of the trigeminus (5th) nerve. Similarly acts mechanical irritation of the stomach, and especially of its serous coat. The pressor action of sensory nerves is only present as long as the brain is intact (E. Cyon). The respiratory variations in the blood pressure which were previously alluded to, appear in part to be in relation with the rhythmical activity of the vaso-motor centre (Schiff).

Many of the facts which have been adduced point to the existence of a complex regulating system, by which the velocity and the pressure of the blood flowing into the capillaries are maintained constant or within the limits necessary to the functional activity of the organs. It is specially to be noticed that a high

pressure in the arterial system, and in the heart, on the one hand, increases the activity of the heart, on the other (through the *nervi depressores*), diminishes the resistance which it has to overcome, by causing a relaxation of the peripheral arteries. Our knowledge is as yet far too incomplete, to permit of our understanding the complete mechanism. (For the regulation of the blood pressure in the brain consult Chap. XI.).

Frequency of the Pulse.

From the facts which have been adduced, it follows that the frequency of the pulse, the height of the blood pressure, and the velocity of the circulation depend upon very numerous influences. The mean frequency of the pulse amounts to seventy-two beats in the minute; in the fœtus, however, it is much greater (184); the pulse falls to the twenty-first year. In old age the frequency again appears to increase.

The frequency of the pulse is very liable to vary; thus strong mental emotions exert a powerful action upon it, probably through the vagi. The following are the influences which chiefly affect the pulse rate. *Temperature:* heat increases, cold diminishes the frequency of the pulse (either by a direct action, or more probably in a reflex manner). *Movement* increases the frequency. *Position of the body:* when the body is vertical, though the muscles be at rest, the frequency of the pulse is greater than when it is horizontal. *Respiration:* during inspiration the pulse is slower than during expiration: further, the frequency of the pulse is greater during digestion than during the intervals between meals, and it is finally greater in persons of the female sex and of small stature than in those of the male sex and of large stature.

Numerous medicinal substances and poisons exert an action on the frequency of the pulse, as soon as they enter the blood. They do so partly by a direct action on the cardiac ganglia, partly by exciting or paralysing the *vagus-centre*, or the fibres of the vagus, especially its terminations in the heart, and they possibly even act on the *accelerating* system. The above-mentioned influences on the pulse may also be due to an action exerted on the vaso-motor apparatus.

APPENDIX.

Emigration.   Diapedesis.

UNDER abnormal conditions both red and colourless blood
corpuscles may leave vessels without rupture of their walls
('Diapedesis'). The escape of the red corpuscles occurs during
stoppage of the venous current. In consequence of the high
pressure thus resulting, first the plasma is pressed out, and then
the blood corpuscles ; these, after being squeezed until all shape
is lost, are pressed out like a fluid mass ; afterwards, they resume
their original form (Cohnheim). The same thing also occurs
under other influences which are not mechanical, for instance,
by the action of salts on exposed vessels (Prussak, denied
by Cohnheim). Colourless corpuscles leave the vessels during
inflammation either alone or together with a few red ones.
After an enlargement of the small arteries and veins has been
caused in a manner which is not yet understood by inflamma-
tory action, and the speed of the current within them has been
considerably lessened, a separation takes place of the colourless
elements, which move slowly along close to the vascular walls,
and at last become stationary, whilst the red ones flow on in the
axis of the vessels. In the veins and capillaries the colourless cor-
puscles are then seen to pass through the vascular walls, dis-
playing amœboid movements, and to appear outside as 'pus cor-
puscles' (Cohnheim). The formation of the above marginal
layer may be explained either by the unequal speed of the
various layers of blood, which would cause the spherical colour-
less corpuscles to roll gradually to the periphery, especially
when the blood stream has become sufficiently slow (Donders,
Cohnheim), or by a peculiar adhesiveness of the colourless cor-
puscles, which causes them, when the current is sufficiently slow,
and they have accidentally fallen against the vascular wall, to

adhere to it (Hering). Whether the passage of the corpuscles outwards happens in consequence of active amœboid movements (Cohnheim) or by a kind of filtration (Hering, Samuel), further, whether the passage takes place through openings (stomata), which exist preformed in the wall of the vessel, between the epithelial cells, is as yet unknown.

CHAPTER II.

SOURCES OF LOSS TO THE BLOOD.

Secretion.

THE term 'secretion' in its widest sense denotes all those processes in which substances quit the blood in an altered or unaltered condition. The products of such processes are called 'secretions,' and may be regarded as of two sorts, viz:—

1. Those liquids or gases[1] derived from the blood, which exude from the internal or external surfaces of the body. Those yielded by internal surfaces (in cavities or canals)—called 'secretions' in the restricted sense—are destined for particular uses (*e.g.* in digestion), and are for the most part again taken up by the blood after undergoing a certain amount of change. Those yielded by external surfaces—called 'excretions'—are, on the contrary, lost to the body, although certain of them (*e.g.* the sebaceous and sudoriparous excretions), have certain functions in connection with the surfaces where they appear.

It will be seen that in their origin there is no difference between secretions and excretions; certainly the fact of their being liberated at internal and external surfaces respectively does not create a fundamental distinction. If we must keep them separate it will be best to regard those substances as excretions which are incapable of further use in the organism and whose retention by it would be harmful. To this class belong certain ultimate results of oxidation—carbonic acid, urea, &c.; and the respiratory and urinary products would, therefore, be the chief excretions. Frequently all the substances given off by the body, irrespective of their origin, are called excretions. If this definition be adopted, we must add to those just mentioned the following, the essential constituents of which are not at all, or only indirectly, derived from the blood:—1. The fæces, *i.e.* the indigestible parts of food mixed with those constituents of the alimentary secretions which are not reabsorbed by the blood-vessels. 2. Epithelial exuviations (*i.e.* the cast-off portions of epidermis, hair and nails). 3. Ova and semen.

[1] Gaseous secretions are treated of in Chapter IV.

2. Those liquids derived from the blood which bathe the tissues of the body,—parenchymatous juices, muscle juice, the fluid moistening connective-tissues, &c.

Inasmuch as the solid portions of the tissues (cells, fibres, &c.) derive the material of which they are composed from the various parenchymatous juices, and therefore immediately from the blood, every constituent of the body may be looked upon as a secretion. This process is, however, so imperfectly understood that we cannot pause to discuss it now. For the same reason we can here only refer, in general, to the secretion of the parenchymatous juices.

I. SECRETION IN GENERAL.

Physical Processes.

All fluids separated from the blood must pass through the walls of closed capillary vessels. It would seem that the only instance, during health, of a fluid passing through ruptured vessels is the menstrual flux : and even this may turn out to be a case of diapedesis. (See p. 81.)

The physical forces which bring about the passage of fluids through membranes are filtration and diffusion.

By filtration we understand the passage of a liquid under the influence of pressure through the pores (not the physical, intermolecular spaces, but the coarser, mechanical interstices) of a body such as a membrane. Just as in the ordinary process of filtering the weight of the substance to be filtered forces the liquid through the filter, so the tension of the bloodvessels forces out some or all of the fluid constituents of the blood; for the pressure of the fluids surrounding the capillaries (parenchymatous juices) is generally less than the pressure of the blood in the vessels.

The amount of the filtered fluid increases with the difference between these two pressures. This difference is made more marked, 1, by relieving the tension in the neighbourhood of the capillaries, as in the withdrawal of the parenchymatous fluids or the reduction of the atmospheric pressure by cupping, &c.; 2, by increasing the tension of the capillary walls, which may be brought about (as was mentioned previously) : *a*, by increasing the blood-pressure all over the body ; *b*, by widening the arteries conducting blood to the part, *e.g.* by relaxing the normal contraction of their circular muscles by the application of heat, or by cutting off the influence of vaso-motor nerves. The converse operations, viz. diminution of blood-pressure, application of cold, and abnormal irritation of vaso-motor nerves will diminish the amount of the filtered fluid. This partly explains the influence of the nervous system upon secretion (see below). Filtration is affected also by the nature of the filtering fluid. True solutions pass through the medium

unchanged. Viscid fluids, such as solutions of albumin, starch and gum, filter less perfectly, a portion only of their contained substances, in amount varying with the pressure, being able to percolate. If indeed the pressure is very slight, the whole is retained on the filter. Under slight pressure, therefore, the blood loses by filtration water, salts, sugar, &c., which form true solutions; while under a greater pressure it is deprived of more or less of its albumin, fibrinogen, &c.

Diffusion (or osmose) is the intermixing of fluids through a membrane, independently of any difference of pressure on the two sides, often even in opposition to hydrostatic pressure. For this purpose it is not necessary that the membrane should be porous, the essential molecular interspaces of a homogeneous membrane being all that are required. (The most homogeneous membranes known are the so-called 'precipitation-membranes' which are formed at the surface of contact when one of two solutions capable of producing a precipitate is allowed cautiously to flow over the other, M. Traube). In diffusion two liquids are required, while in filtration it is only necessary to have a liquid on one side of the membrane, the other being presented to the air or to a vacuous space. Diffusion, moreover, can only take place between liquids of different kinds, while filtration may occur between those of the same kind, provided that each is subjected to a different pressure. The essential condition of diffusion is that the membrane should be saturated simultaneously by both liquids; the object of the process is the complete chemical equalisation of the fluids on the opposite sides of the membrane. According to the latest researches the passage of a substance through a membrane (Endosmose) takes place, if there is on the other side of the membrane a liquid capable of dissolving the substance and having an affinity for it; and if the molecules of the body are somewhat less than the molecular interstices of the membrane. Endosmose takes place more quickly, the greater this affinity ('Endosmotic force'), the smaller the molecules of the substance, and the larger the interstices (M. Traube). Endosmotic force is very great in the case of strongly hygroscopic substances. Certain complex bodies of great molecular weight (p. 30 *et. seq.*) are incapable of diffusing through most membranes on account of the large size of their molecules. Such substances are albumin, hæmoglobin,[1] gum, &c., which have been denominated 'colloids' by Graham, on account of their non-existence in a crystallised form, in contra-distinction to 'crystalloids,' or substances which admit of crystallisation. Other writers (Vierordt, Jolly) consider the essential element in the process of diffusion to be the interchange between a portion of the diffusing substance, and·an amount of the solvent liquid on the other side of the membrane; and the quantity of the solvent liquid which passes through for every unit of weight of the substance they call its 'endosmotic equivalent.'

As the blood is everywhere surrounded by fluids of a differ-

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[1] Although hæmoglobin is crystalline, it cannot be said to belong to the crystalloid group, as it does not diffuse; without doubt, had Graham been acquainted with this, the only known crystallisable, yet indiffusible body, he would have chosen a more appropriate name for the group.

ent chemical composition, and under a lower pressure than itself, it is plain that in nearly all cases of secretion both filtration and diffusion must play a part.

The purely physical processes of filtration and diffusion can only yield fluids containing the constituents of liquor sanguinis in various proportions. It has not been ascertained with certainty whether such simple separations occur. The nearest approach to them are the so-called transudation fluids, viz. the fluids found normally in the various cavities of the body (*e.g.* in the pericardial, peritoneal and pleural sacs, in the cerebral ventricles, &c.); and the pathological fluids of dropsical cavities and œdematous tissues. Their principal constituents are water, salts, sugar, urea, varying amounts of albumin, fibrinogen, and sometimes also fibrinoplastin. The presence of fibrinogen may be demonstrated by the setting-in of coagulation on the addition of fibrinoplastin and the fibrin-ferment (*e.g.* in the form of a well-squeezed blood-clot. If the transudation-fluid contains at the same time fibrinoplastin, coagulation occurs spontaneously on withdrawal from the body; but, as a rule, only slowly, on account of the fibrinoplastin being present in such small quantities.

It has lately appeared very probable that the fluids found in the various cavities above mentioned should, in part at least, be regarded as lymph (Chapter III.); for not only have lymph-corpuscles been seen floating in them, but direct communications have been traced between the cavities containing them and the lymphatic vessels (von Recklinghausen).

Chemical Processes.

Most secretions contain, in addition to the substances which are common to them and the blood, certain specific constituents, for the production of which the above-mentioned physical processes cannot alone account. It is necessary, therefore, to assume that certain chemical changes take place in the transuded fluids, the seat of which, or at least the impulse to which, must most probably be sought for in the cells with which the various secretions come into contact. Such cells are, in the case of parenchymatous juices, the cells or corpuscles of the tissues in which they arise; in the case of free secretions, the gland-cells.

The only difference therefore between parenchymatous

and free secretions appears to be that the former remain en-
closed in a fine cellular network, while the latter pass through
a thin layer of cells (in the glands) and so quit their place of
origin.

As the specific constituents of the various secretions belong,
for the most part, to a class of bodies whose nature and origin are
unknown, nothing can with certainty be said about the nature of
the chemical processes supposed to take place in the cells of the
various tissues and glands. Certain of these specific substances
are, however, undoubtedly the result of the oxidation of some
of the constituents of blood : and, as secretion is accompanied
by a manifestation of energy, viz., as Ludwig has directly
proved in the case of the salivary glands, by an evolution of
heat, it is probable that all the chemical processes of secretion
are merely processes of oxidation. This is further supported by
the facts that, during the production of a secretion rich in its
characteristic elements, more of the oxygen conveyed through
the arteries to the gland is used up, as is indicated by the darker
colour of the venous blood ; and that secretion becomes im-
possible as soon as the supply of arterial blood is prevented,
notwithstanding that the other necessary conditions are fulfilled.
(Consult the section on Saliva).

In certain secretions the specific constituents are derived
from the disintegration of cells. This is known to be the case
with milk and the mucous, salivary and sebaceous secretions;
and it is probably also the case with others.

Organs of Secretion.

Free secretions are generated in special organs. The
simplest form of secreting organ is a membrane provided with
blood-capillaries on the one side and a layer of epithelium cells
on the other ; it has, moreover, nerves, the terminations of which
are probably in direct connection with secreting cells. Such a
form of glandular apparatus is that which serves for the secre-
tion of the fluids filling the serous and synovial sacs, bursæ and
sheaths. Most secretions, however, require a larger surface
than a simple smooth membrane can afford. To supply this
the membrane presents a single or branched, tubular or saccu-
late involution of its surface, upon which the secretion is poured

out (mucous membrane, skin). Every layer of the originally smooth membrane follows the course of the sacculations; an examination of any part, therefore, would show, externally, a supporting stroma of connective tissue containing blood-vessels, and often also muscular fibres; and internally an epithelium, the cells of which often become modified in form at the bottom of an involution, passing there into special secreting cells. Such an involuted secreting surface is called a *gland.* All transudations through the sides of the blood-vessels must, therefore, pass through the layer of cells before occupying the hollow of the gland as a secretion, or reaching the surface, the sacculation of which forms the gland. There is another way in which the secreting surface may be increased, viz., by processes (villi), or projections such as are seen in synovial membranes.

If the involutions of the glandular surface are branched, the gland is said to be 'compound;' if they, or their branches, are like tubes or cylinders, the gland is called 'tubular' (sweat glands and gastric follicles, kidneys, testicles, &c.); if like sacs, 'racemose' (mucous, sebaceous, and salivary glands, &c.). In the case of compound glands, the tubular structure which leads into the gland, and into which the gland-products are emptied, is called the 'excretory duct.' This is frequently provided with an enlargement which serves as a reservoir (urinary bladder, vesiculæ seminales); or it may be connected with such a reservoir by means of another duct (gall-bladder). The so-called 'ductless' glands (spleen, lymphatic glands, follicles, suprarenal capsules, thymus, thyroid) are really not glands; they will be discussed in Chapters IV. and VI.

Influence of Nerves on Secretion.

In every act of secretion there is probably a nervous influence at work. This has been distinctly proved in many cases. It may assume the form of a first impulse to the act; or it may be evidenced by a quantitative or a qualitative alteration of the products, brought about by nervous excitation.

As in several glands (*e.g.* in the salivary glands, Bernard) the influence of the nervous system on secretion is connected with that on the blood-circulation through the gland, we might be inclined to explain the former as dependent upon the latter. The nervous system may influence secretion by its action on the circulation, which, leading to dilatation or narrowing of the arteries, may bring about, 1, changes of pressure in the gland capillaries, and, therefore, filtration-changes; 2, changes in the

chemical processes dependent on the greater or less quantity of oxygen brought to the gland. Inasmuch as nervous influence may bring about a secretion which is in abeyance (in glands cut out of the body, Ludwig), even when the circulation is suspended, and as secretion may proceed when filtration is impossible, we must conclude that the influence of the nervous system upon secretion cannot be explained by its mere action upon the circulation. (By preventing the escape of a secretion the pressure in the excretory duct of a gland may, under nerve-stimulation, be raised above that in the arterial branches supplying the gland, and yet secretion proceed, Ludwig). Recently, anatomical changes have been discovered to occur in the glandular substance under the influence of nerve irritation (Heidenhain; see Saliva). It must be assumed, therefore, that, besides the vaso-motor, there are other specific ' secretory ' nerve fibres, which have a direct, but as yet unintelligible, influence on the processes of secretion.

The influence of the vaso-motor nerves, apart from that of the proper secretory fibres, is conclusively proved (Bernard) by the coincidence of secretion- and circulation-changes, which has already been pointed out. From the nature of the case their influence is principally upon the process of transudation ; and they, therefore, affect the quantity and state of concentration of the secretion. The influence of the nervous system upon the chemical processes of glands, due to its power of modifying the supply of oxygenated blood to them, is uncertain, although we know that a supply of such blood is necessary for continuous secretion. (A gland cut out from the body, when its nerves are stimulated, yields its secretion only at first, even though by the production of artificial œdema a rich supply of fluid has been stored up within).

An attempt has in recent times been made to prove anatomically the existence of secretory nerves. The statement upon which this attempt is founded, that a direct communication exists between nerve-fibres and secreting cells (Pflüger), has, however, been often contradicted.

II. INDIVIDUAL SECRETIONS.

A. Parenchymatous Tissues and their Secretions.

The methods hitherto used of obtaining the fluid secreted by parenchymatous tissues have failed to yield it pure enough, or in sufficient quantities, for the purposes of examination. They consist either in expressing the juices from tissues which

have been deprived, as far as possible, of their blood, or in extracting the constituents of those juices one by one by means of various solvents (ether, alcohol, water, acids). Our knowledge of the composition and formation of the parenchymatous secretions is, therefore, extremely scanty. It is often even doubtful whether the substances thus obtained from a tissue should be referred to its fluid or its structural elements. We can only suppose in reference to their origin that their peculiar constituents (gelatin, fat, colouring matters, &c.) are formed from the fluids which transude from the blood-vessels by the influence of the cells of the tissues, and probably under the control of special (trophic) nerves (Chapter IX.). It is further assumed that the transuded fluids are yielded in excess, which excess is returned to the blood by the lymphatics which absorb it (Chapter III.). The specific substances which are formed are in part insoluble, and become the structural elements of the tissues. Hence it follows that a purely chemical consideration of the fluid and formed constituents of parenchymatous tissue is not yet possible, and that the whole history of the development of the tissues can only be treated of from a morphological point of view. It will only be necessary, therefore, in this place, to state briefly, without any attempt at classification, the facts which have been ascertained respecting the chemical composition of the various parenchymatous tissues.

1. *Osseous Tissue.*—Pure osseous tissue (after the removal of the periosteum, marrow, &c.) contains a great excess of inorganic salts. Perfectly dried bones (bones contain about 2 per cent. of water) exhibit a very constant composition, which is different for different kinds of animals. In man there are 68 parts per cent. of salts, and 32 per cent. of organic matter (Zalesky). The salts are, 84 per cent. of tribasic calcium phosphate ($Ca_3 2(PO_4)$), 1 per cent. of tribasic magnesium phosphate ($Mg_3 2(PO_4)$), 7·6 per cent. of other salts of calcium ($CaCO_3$, $CaCl_2$, $CaFl_2$), and 7·4 per cent. of alkaline salts ($NaCl$, &c.).

The organic portion consists almost entirely of a *gelatigenous* substance, which yields gelatin on boiling, especially after the addition of acids.

The osseous tissue of compact and spongy bones presents the same composition. This constancy of composition has led to the assumption that the

organic portion is not merely mechanically impregnated by the mineral, but that the two are chemically combined (Milne-Edwards jun., Zalesky).

Dilute acids deprive bone of its salts, and leave behind the animal portion, which is soft and resembles cartilage. Subjection to heat, on the contrary, destroys the animal matter, leaving a white, porous, inorganic mass (calcined bone). In both cases the bone retains its original external shape.

Connected with bone are the other calcareous tissues, *e.g.* teeth. Enamel, which contains very little water, possesses only 4 per cent. of organic matter, and is analogous to bone in its composition.

Nothing is known about the formation and regeneration of bone-tissue, except the morphological appearances presented in the various stages.

2. *Cartilaginous Tissue.*—Besides water and the constituents of the corpuscles, cartilage contains chiefly *chondrogenous* substance (p. 36), elastin (p. 35), and small quantities of inorganic salts.

Nearest to cartilage stands the tissue of the cornea, which on boiling yields a body resembling chondrin: it contains, in addition, much fibrinoplastic substance.

3. *Connective Tissue.*—In connective tissue the following elements have been recognised (Kühne):—(1.) The substance of the fibrillæ, a gelatigenous substance. (2.) An interfibrillar cementing substance, which can be extracted by lime-water or baryta-water (Rollett), the extract containing mucin. (3.) elastin. (4.) Corpuscles, composed mainly of albuminous elements, and frequently containing fat. In fœtal and some other tissues the gelatigenous substance is replaced by a mucin-yielding substance.

4. *Muscular Tissue.*—See Chapter VIII.

5. *Nervous Tissue.*—See Chapter IX.

B. Fluids of Cavities.

These fluids are not secreted by glands, but by the epitheliated membrane ('serous membranes,' &c.) lining the cavities where they are formed. From their composition they are regarded as simple transudations, the essential constituents of which have already been enumerated (p. 86). Their quantitative relations are extremely various and cannot be referred to here. The following fluids may be regarded as simple transudations:—the cerebro-spinal fluid, the aqueous humour,

and perhaps also the amniotic and allantoic fluids.   The peri-
cardial, pleural, and peritoneal fluids were formerly placed
in the same category; but since they communicate directly
through apertures with the lymphatic vessels (von Reckling-
hausen, Oedmansson, Ludwig and Dybkowsky), they must be
considered as lymph (Chapter III.).

The following fluids of cavities have special constituents:

1. Synovia contains, in addition to the products of transu-
dation, mucin (0·2 to 0·6 per cent.) and fat (0·06 to 0·08 per
cent.).   Numerous exuviated epithelial cells are also present.

2. The fluids of bursæ mucosæ and synovial sheaths contain
a gelatinous material which has not yet been investigated.

The way in which the secretions of this class are used up
and replaced is not understood.

C. Glandular Secretions.

I. ALIMENTARY SECRETIONS.

1. *Mucus.*

The mucus of the alimentary canal is secreted by glands
which are lined by an epithelium resembling that of the region
in which they are situated.   In the mouth, pharynx, and
œsophagus, the glands are small and racemose, and contain
scaly epithelium; in the stomach (especially in the neighbour-
hood of the pylorus) and in the intestine, they are simple, or
slightly compound and tubular, and the epithelium is cylin-
drical.   Mucus is a clear, slimy, ropy, alkaline fluid, consisting
essentially of a solution of mucin, and also sometimes of albumin,
in which the normal salts of the blood, especially NaCl, are dis-
solved.   The mucus of the intestine contains, in addition, certain
ferments which confer upon it special properties, and is, there-
fore, considered separately under the name of intestinal juice
(see below).   As a rule, mucus contains morphological elements
in the form of (1) small, round, nucleated cells, resembling
the colourless blood-corpuscles—the so-called mucous corpuscles
—which are considered to be the young cells of the mucous
glands; (2) fragmentary or entire cells of scaly epithelium from
the mucous membrane, frequently adhering together by their

edges as in their natural condition. The slimy nature of mucus fits it admirably for the purpose of lessening the friction between the walls of the alimentary canal and their contents.

Pure mucus may be obtained from the mouths of animals after ligaturing the ducts of all the salivary glands. It may be inferred from the morphological elements of mucus that mucin arises only through the disintegration of gland-cells (compare the salivary, sebaceous, and milky secretions). The influence which nerves exert upon the secretion is yet unknown.

As mucin does not appear to be capable of reabsorption, it most likely all passes out of the body in the fæces, while some of the remaining constituents of mucus probably find their way back into the blood.

2. *Saliva.*

The three different kinds of saliva from the parotid, submaxillary, and sublingual glands are very watery, colourless alkaline secretions of low specific gravity (1·004—1·009). Besides the usual products of transudation (among which are found very small quantities of albuminous bodies, albumin and globulin), they contain, as specific constituents, (*a*,) mucin, of which the sublingual saliva possesses the most, the submaxillary less, and the parotid least ; (*b*,) a hydrolytic ferment, *ptyalin*, which converts starch into dextrin and sugar, this conversion taking place rapidly if the starch is in the form of a paste, and still more rapidly if it is subjected to the temperature of the body; (*c*,) sulphocyanides (potassium-sulphocyanide). Moreover, saliva, and especially, as it would seem, sublingual saliva (Donders), contains morphological elements—salivary bodies— resembling closely mucous corpuscles ; these ' salivary cells ' enclose granules which exhibit active molecular movements. Mixed saliva contains also mucus and exuviated squamous epithelial cells from the cavity of the mouth.

In order to obtain the various kinds of saliva separately, use is made, in man, of pathological salivary fistulæ ; except in the case of the parotid gland, where the saliva may be collected through a fine tube introduced into Steno's duct, which opens in the side of the cheek opposite the second or third upper molar tooth. In the lower animals artificial fistulæ may be established. Ptyalin may be thrown down mechanically (p. 35) by causing a precipitation of calcium phosphate insaliva; it may then be extracted from the precipitate by water, and re-precipitated from the watery solution by alcohol. It is not an albuminous body (Cohnheim). The power of converting starch into sugar belongs to each of the three kinds of human saliva; but it is best

shown in mixed saliva formed in the cavity of the mouth by the admixture of saliva from all the glands with mucus. In the lower animals, however, the three kinds do not all possess this power; for, in general, the three kinds of saliva are secreted in individual animals in proportions regulated by the food they usually take. The conversion into sugar takes place very rapidly, and is not prevented by the presence of a moderate amount of acid—a circumstance which is of importance in digestion. A given quantity of saliva cannot convert an indefinite quantity of starch into sugár (Paschutin). Potassium sulpho-cyanide, CN.KS, the presence of which may be demonstrated by the blood-red colouration which occurs on the addition of ferricchloride, is not a constant constituent of saliva, and is found most frequently in mixed saliva from the mouth, especially if the teeth are decaying.

As an example of the quantitative composition of saliva, the following analysis of human mixed saliva may serve (Bidder & Schmidt). In 1,000 parts—water 995·16, solid constituents 4·84, containing epithelium 1·62, soluble organic matters 1·34, inorganic matters 1·82, almost one half of the last being alkaline chlorides.

Secretion.

The secretion of saliva is, as may be demonstrated, under the influence of the nervous system, which influence has been more fully investigated in this case than in that of any other secretion in the body. Without the operation of this influence secretion is completely inactive (C. G. Mitscherlich, Ludwig). During life, the excitation of secretory nerves would seem to take place always in one of two ways: either, in a reflex manner, on irritation (1) of the sensory and gustatory nerves of the mouth, (2) of the vagus, probably of those fibres proceeding from the digestive apparatus (Oehl, though this is doubted by von Wittich, Nawrocki); or on (voluntary) stimulation of the nerves to the masticatory muscles. Saliva is therefore secreted (a) on irritation of the cavity of the mouth by sapid substances or mechanical, chemical, thermal, or electrical stimuli, (b) in certain conditions of the stomach (nausea), and (c) during the movements of mastication. The centripetal fibres, which, on irritation, lead reflexly to secretion, run in the course of the trigeminus, the glosso-pharyngeus, and the vagus. The secretory fibres run in the course of the facialis, the trigeminus, and the sympathetic.

Irritation of sensory nerves far removed from the glands (e.g. of the central end of the ischiatic nerve) may also cause, by reflection, the secretion of saliva (Owsjannikow & Tschiriew).

Among the secretory nerves we must distinguish two species (Bernard, Eckhard, von Wittich) which, on irritation, produce differences, not only in the character of the secretion, but also if the vaso-motor phenomena: nevertheless, as was pointed out on p. 89, we are not entitled to explain the former as dependent upon the latter. Irritation of fibres of the first kind induces narrowing of the arteries supplying the gland, the blood reaching the veins in small quantities and very dark in colour; at the same time it yields small amounts of an extremely tough and often gelatinous saliva, very rich in its specific constituents, and especially in mucus. The second species of nerve-fibres appears to cause widening of the vessels proceeding to the gland, for, when irritated, the blood flows in such quantity into the veins that they pulsate, and it is of a colour almost as bright-red as that in the arteries; the saliva secreted under these circumstances is copious, and, as it contains but small quantities of specific constituents, very fluid. The fibres of the first kind run, to all the glands, in nerves of the sympathetic system. Those of the second kind arise in the facialis and afterwards pass into the course of the trigeminus; viz., in the case of the parotid gland, through the nervus petrosus superficialis minor (of the facial), to the otic ganglion, and thence to the auriculo-temporal branch of the trigeminus (Bernard, Nawrocki); and, in the case of the submaxillary and sublingual glands, through the chorda tympani (of the facial) to the lingual branch of the trigeminus, whence, after a brief course, they pass, some directly, others through the submaxillary ganglion, to the gland (Bernard).

Even if it be assumed that the copious trigeminal-saliva secreted under great pressure deprives the gland of the same quantity of specific constituents in a unit of time as the scantier sympathetic-saliva (Bernard), the vaso-motor effect would yet be insufficient to explain secretion; for the pressure in the glandular ducts may rise higher than that in the blood-vessels (p. 89), and secretion may be brought about, under nerve-stimulation, after the cessation of the blood-stream through the gland (Ludwig, Giannuzzi). Some other mechanism, therefore, as yet unknown, must lie at the root of the process; and here the reader may be reminded of the assumed connection (according to Pflüger) of nerve-fibres with glandular cells. The following appearances (Heidenhain) indicate yet more clearly a specific effect of secreting nerves: in the acini of those salivary glands, the secretion of which contains mucin, two species of cells are to be found: (1) nucleated, wall-less, 'protoplasm-cells,' containing much albumin, but no

mucus. In many glands they lie thickly scattered about; in the submaxillary of the dog they form a crescent-shaped series on one side of the acinus, while in the cat they occupy the whole circumference. (2) Shining ' mucus-cells,' containing mucus enclosed in a cell-wall. After continued irritation of the secreting nerves, especially of those of the cerebro-spinal series, protoplasm-cells alone are found, undergoing rapid multiplication, while the remains of mucus-cells are recognisable in the secretion. It is evident, therefore, that, during secretion, a conversion of protoplasm-cells into mucus-cells through the ' mucin-metamorphosis' of their contents has taken place; the protoplasm-cells are replaced by the fission of those left, and the mucus-cells disintegrate. The cell-contents of the acini are, therefore, constantly in course of renovation, and a continuously stimulated gland resembles in appearance that of a recently-born animal. Some of the young protoplasm-cells appear to mingle with the secretion as salivary corpuscles (p. 93). In the submaxillary gland of the rabbit, which yields a secretion containing no mucus, protoplasm-cells only are found. The buccal mucous glands (p. 92) resemble in their relations the mucus-yielding salivary glands. According to a later theory (Ewald) regeneration of the glandular contents does not consist in destruction of the mucus-cells and their reformation out of protoplasm-cells, but simply in the liberation of the mucus contained in the former, whereby they again take on the appearance of protoplasm-cells. The temperature of salivary glands may be raised 1·5° C. during secretion (Ludwig).

As there exist poisons which paralyse the secretory fibres of the chorda tympani without interfering with those which cause vascular dilatation, *e.g.* atropia (Heidenhain), it is probable that the former are not identical with the latter. The salivary glands, therefore, possibly receive four different varieties of centrifugal nerve fibres capable of influencing the secretion, viz. separate vaso-motor and separate secretory fibres in each of the two classes of nerves (cerebro-spinal and sympathetic) going to them.

Salivary secretion brought about by reflex irritation of nerves yields constantly a very fluid (trigeminal) saliva. In the case of the submaxillary gland the centre for this reflex action, when stimulation proceeds from the nerves of taste or from the stomach, is probably in the brain—the medulla oblongata—as irritation of that organ produces a secretion of saliva so long as the glandular nerves are intact (Eckhard). In the case of stimulations other than gustatory applied to the mucous membrane of the mouth the centre of reflection is the submaxillary ganglion. This is proved by the fact that, after section of the truncus tympanico-lingualis, stimulations of the former kind no longer produce any effect, while those of the latter kind operate as usual (Bernard). We must suppose, therefore, that the submaxillary ganglion is a centre presiding over secretion, which may be stimulated to reflex activity

through certain fibres running from the tongue in the course of the lingualis, and leaving that nerve finally to reach the ganglion. On the contrary the fibres coming from the brain, and conducting reflected impressions which originated in the gustatory nerves, reach the ganglion by way of the facialis, chorda tympani and tympanico-lingualis, and probably simply traverse it (Bernard).

It is, moreover, worthy of remark that, on cutting away the submaxillary ganglion, with the exception of the fibres passing through it from the tympanico-lingualis, or on poisoning the blood flowing through the gland with curare, a continual secretion is induced, which can only be increased by the stimulation of sapid substances (Bernard). This 'paralytic' secretion appears also in the gland of the opposite side (Heidenhain). A continuous secretion, moreover, occurs if the tympanico-lingual trunk has been cut through for a long time; in which case the sympathetic fibres alone are able (in the manner before indicated) to modify the secretion. An explanation of this paralytic secretion has been sought partly in the supposed existence of inhibitory nerves, and partly (Heidehain) in some effect of the stagnating secretion. The paralytic secretion soon ceases, in consequence of the degeneration of the glands.

The amount of saliva secreted in twenty-four hours has been variously estimated at from $\frac{1}{2}$ to 2 kilog. The fluid constituents of saliva, with the exception of the mucin, are probably for the most part reabsorbed in the alimentary canal (Chap. III).

3. *Gastric Juice.*

Gastric juice is the secretion of the tubular glands, which, closely packed and swollen inferiorly, crowd the gastric mucous membrane. Gastric juice is a thin, clear, colourless, acid fluid which is mixed in the stomach with gastric mucus. Its specific constituents are: (*a*) free hydrochloric acid; this may, without prejudice to the effect of the gastric juice, be replaced by lactic acid, which is generally formed in the stomach during digestion (Chap. III.): (*b*) a hydrolytic ferment *pepsin* capable of splitting up albuminous bodies. Pepsin has the property in acid solutions of quickly dissolving coagulated albuminous substances at the temperature of the body. Solution, preceded by swelling up of the albumin, takes place most rapidly under that degree of acidity which can produce the quickest swelling up (*e.g.*, for the fibrin of ox, 0·8 to 1 grm. HCl per litre, Brücke). With the same

quantity of acid, however, it takes place more quickly the more pepsin there is in the solution, until a maximum is reached, beyond which the solution cannot be hastened. A certain quantity of pepsin has the power of dissolving fresh amounts of albumin, if the acid used up be continually replaced. The changes which albuminous bodies undergo during solution are as yet little understood. At first they appear to retain their original properties. They are precipitable by heat (provided that, before being subjected to the action of the gastric juice, they had not been coagulated by heat, in which case the swelling up and solution generally take a longer time), and also, for some time, by neutralization with alkalies. They are therefore at this stage converted into syntonin. After a longer period they lose the power of being precipitated by heat, alcohol, mineral acids and certain metallic salts, and are called in this condition *peptones.* Peptones have, moreover, a far greater power of diffusion (p. 85) than ordinary albuminous solutions (Funke). Dissolved albuminous bodies undergo the same transformation under the influence of the gastric juice: Gelatin is, by the action of gastric juice, converted into an ungelatinizable modification. All these changes must, most probably, be regarded as hydrolytic decompositions. As a smaller amount of peptones is obtained, during continued pepsin-digestion, than corresponds to the albumin used, it would seem that peptones are capable of still further decomposition, the products of which are, however, yet unknown (Kühne). Under the action of the gastric juice, even when neutralised, milk is firstly curdled and the precipitate of casein afterwards digested. It is supposed that pepsin quickly converts milk sugar into lactic acid ; milk, however, coagulates even when the gastric juice is alkaline. Processes of fermentation and putrefaction are generally hindered by the gastric juice.

The active properties of the gastric juice are suspended by the same influences as deprive ferments of their activity (boiling, concentrated acids, many metallic salts, strong alcohol, &c.) Concentrated salt-solutions delay the solution of the albuminous bodies, as they hinder their swelling up. In the same manner solution is delayed if the swelling up be prevented by tying thread tightly round the pieces of coagulated albumin.

Bile also retards solution, not only by neutralising the acid, but also by hindering the swelling up (Brücke), and precipitating the peptones (Bernard).

It has been sought to explain the interference of bile with gastric digestion (Burkart) in the fact that a precipitation of glycocholic acid occurs on the addition of bile to acid gastric juice, the pepsin being supposed to be carried down mechanically in the process (p. 35). It is urged, on the contrary (Hammarsten), that bile which contains only taurocholic acid also destroys gastric digestion; that, further, non-albuminous gastric juice is *not* precipitated on the addition of bile, and yet loses its digestive properties on admixture with that body. Pepsin is not destroyed in the process, but can be again isolated in an active condition. The power which bile possesses of preventing digestion depends principally upon the fact that it hinders the swelling up of the albuminous bodies; it precipitates the peptones already formed, even when the fluid is decidedly acid (Brücke, Schiff). The prevention of the process of swelling up is said to depend upon the combination of the bile-acids with albumin (Hammarsten). Glycocholic acid does, however, possess the power (Burkart) of precipitating pepsin. The secretion of Brunner's glands also renders the gastric juice inoperative (Schiff).

Natural gastric juice is obtained from pathological, or (in the case of the lower animals) artificial gastric fistulæ; and also by causing sponges attached to a string to be swallowed and, after a time, withdrawn from the stomach. Artificial gastric juice is prepared by infusing fresh or dry gastric mucous membranes with water or (von Wittich) glycerin, and then adding hydrochloric acid (0·1 p. c.); or, also, by dissolving pure pepsin, prepared according to the method on p. 35 in water and acid. Hydrochloric acid may be replaced by lactic acid (which in equal amounts is less effective), or by oxalic, phosphoric, or acetic acids, but the activity of the gastric juice is thereby diminished.

The gastric juice of the dog, free from saliva, contains, as the mean of a number of experiments, in 1,000 parts :—Water 973·1, pepsin (and peptone) 17·1, free hydrochloric acid 3·0, salts 6·8 (Bidder and Schmidt).

Secretion.

The following has recently been made out with regard to the structure of the gastric glands (Heidenhain, Rollett). The glands contain two sorts of round cells : (1) the smaller, so-called 'Hauptzellen' (Heidenhain), or 'adelomorphous cells' (Rollett), which fill the greater part of all the glands, and are alone found in certain glands, occurring especially in the pyloric region (the 'gastric mucous glands' of earlier authors); (2) the larger, so-called 'Belegzellen' (Heidenhain), or 'delomorphous cells' (Rollett), which occur, almost without exception, only near the bottom of the glands at the sides. During secre-

tion (in the process of digestion) the glands, and especially the smaller cells previously referred to, at first swell up strongly, and afterwards return to their former size (Heidenhain). Pepsin is formed in the gastric glands, whence it can be obtained by water in the form of a neutral solution, or, more easily, by the action of dilute hydrochloric acid. It is probable that, during life also, it is extracted from the cells by some acid fluid. Nevertheless the glands themselves very seldom exhibit an acid reaction, while the surface of the gastric mucous membrane is covered with a strongly acid gastric juice. The acid is, however, formed in the glands; for, if the surface of the mucous membrane is neutralised by means of calcined magnesia, then washed with water and allowed to stand, an acid reaction again appears after some time (Brücke). It must be supposed, therefore, that the gastric glands form pepsin and an acid, but get rid of the latter (charged with pepsin) at once at the surface. The forces which effect these operations are not understood; nor is the origin of the free hydrochloric acid; for we can scarcely suppose that it results from the decomposition of some salt (perhaps calcium chloride, Smith) by lactic acid. Probably the simultaneous alkaline formation in the pancreatic secretion is closely connected with this acid formation (Meissner). What part each of the two kinds of glandular cells takes in the formation of pepsin and acid is yet in dispute. While the origination of pepsin used to be ascribed to the larger glandular cells, it has recently been maintained that the smaller variety are the pepsin-formers, because the latter more easily disintegrate under the influence of hydrochloric acid when warm than the former, and snippings from the surface of the gastric mucous membrane digest the more quickly the greater the number of the smaller kind of cells they contain (Heidenhain, Ebstein and Grützner). Others, on the contrary, hold to the former opinion, chiefly because the glands in the pyloric end of the stomach, which contain the smaller cells only, do not yield an infusion capable of digesting foods, if the secretion of the larger cells is absent (Friedinger, von Wittich, Wolfhügel).

Secretion of gastric juice appears to occur only under the influence of the nervous system exerted in a reflex manner (see Saliva). It ceases when the stomach becomes empty; but re-

commences when it is filled with substances (food) which mechanically irritate it; and, probably also, on irritation of the mucous membrane of the mouth. The saliva which is swallowed seems to be concerned in this stimulation (Rollett). Secretion appears to be independent of the integrity of the nerves (vagi, &c.) running to the stomach; the central organs, therefore, of a portion of the secretory nerves must be sought for in the walls of the stomach itself (Brücke, Ravitsch). During secretion a reddening of the mucous membrane occurs, and probably, therefore, a dilatation of the glandular vessels, similar to that which takes place in the secretion of saliva.

The secreted gastric juice is, probably, for the most part, re-absorbed in the intestines (Chap. III.). Small amounts of pepsin are, therefore, found in various fluids of the body, *e.g.* in the parenchymatous juices of the muscles, in urine (Brücke). The acid of the gastric juice is neutralised by the alkaline in-testinal secretion. No serviceable determination or estimation exists of the amount of gastric juice secreted.

4. *Bile.*

Bile is a neutral or weakly alkaline, mostly viscid, bitter fluid, varying in colour from yellow, brown, or green to black. Its specific constituents (apart from the mucus which origi-nates in the gall-bladder and ducts) are:—(1) the sodium salts of two conjugate acids (so-called ' bile-acids '), viz. glyco-cholic acid (called also cholic acid) and taurocholic acid (called also choleïc acid). The former is compounded of nitrogenous glycocine (p. 24) and non-nitrogenous cholic acid (p. 16), the latter of taurine (which contains nitrogen and sulphur) (p. 25) and cholic acid; (2) cholesterin (p. 17), held in solution by the salts of the bile-acids; (3) products of decomposition of lecithin, viz. choline or neurine (p. 21), glycerin-phosphoric acid (p. 19); (4) urea (Popp); (5) colouring matters, es-pecially one of a reddish-yellow colour, bilirubin (cholepyrrhin, bilifulvin); another of a green colour, biliverdin (p. 29) perhaps only a derivative of the former, and one called urobilin (p. 29); (6) small quantities of fats and soaps; (7) a sugar-forming ferment (J. Jacobson, von Wittich).

Bile may be obtained from the gall-bladder after death and, during life,

in the lower animals by means of artificial biliary fistulæ, which may, at the same time, be used to determine the amount secreted in a given time. The colour of bile varies much under different physiological, and, still more, under different pathological, conditions, and in different classes of animals. In the air yellow bile becomes green through the oxidation of bilirubin to biliverdin. The bile of vegetable-feeding animals is green while in the gall-bladder. The salts of the bile-acids may be easily obtained by evaporating bile, extracting with alcohol, decolourising the extract by means of animal charcoal, and adding ether. When prepared in this manner, they are obtained in the form of a resinous precipitate, which becomes crystalline on being kept in a mixture of alcohol and ether ('crystallised bile'). The two bile-acids are present in various proportions; in man, amphibia, and fishes, taurocholic acid predominates, as also in many mammals and birds: in others (*e.g.* in pigs, kangaroos), it is the glycocholic acid which predominates. The cholic acid contained in the bile-acids is replaced in various animals, by other, allied acids (p. 16), *e.g.* in the goose by chenocholic acid, in the pig by hyocholic acid, in guano by guanogallic acid; and the bile-acids bear different names accordingly (taurochenocholic acid, hyoglycocholic acid). The bile-acids rotate the plane of polarisation to the right, cholesterin to the left (Hoppe-Seyler).

Human bile contains in one thousand parts, water 822·7–908·1; salts of the bile-acids 107·9–56·5; fat and cholesterin 47·3–30·9; mucin and colouring matters 23·9–14·5; ash 10·8–6·3 (von Gorup-Besanez).

Secretion.

The formation of bile takes place in the so-called *lobules* (*acini*) of the liver. Each acinus contains, like the whole liver, arterial blood, which is brought by the *hepatic artery*, and venous blood, which is conducted through the *portal vein* from the capillaries of the stomach, intestine, pancreas and spleen; and each furnishes venous blood to the *hepatic vein.* .

The terminal branches of the portal vein (*interlobular veins*), and of the hepatic artery, which lie at the periphery of the lobule, are connected with the initial branches of the hepatic vein (*intralobular veins*), which start from the centre by a close, interlacing capillary network, whose meshes are crowded by the large, round, glandular *cells* of the liver. These liver-cells are so arranged (Hering) that they form the wall of the finest gall-passages, often as few as two only occurring in a transverse section. These passages open into an interlobular network surrounding the acini, whence springs the *ductus hepaticus*, which, after giving off a lateral branch, the *ductus cysticus*, to a reservoir, the *gall-bladder*, opens into the duodenum as the *ductus choledochus.* The blood of the portal vein, which has previously traversed one capillary system, and which is now for the second time distributed over an enormous vascular area, must flow extremely slowly in the capillaries of the liver.

Bile-formation takes place continually. It would seem that, during the intervals between periods of digestion, the secretion is conveyed through the cystic duct to the gall-bladder, and there stored up ; but that, during digestion, it is poured, both directly from the liver, and also from the gall-bladder, into the intestine. The formation of the specific constituents takes place in the liver-cells. That these constituents are not simply separated from the blood, is shown by the fact that, neither under ordinary circumstances, nor when secretion is prevented (by extirpation of the liver) can they be detected in the blood flowing to the liver.

On the contrary, they rapidly appear in the blood if the outflow of the bile from the liver is prevented by the stoppage of the excretory duct, and the pressure in the gall-passages by this means raised ; a very slight pressure is all that is required to effect this return into the blood ; biliary colouring matters, cholic, glycocholic, and taurocholic acids, may then be detected in the urine (Hoppe-Seyler), and the first colours the urine brown, and the skin and mucous membranes yellow—Jaundice. Other colouring matters also, which appear in the gall-passages under pressure, are reabsorbed and colour the mucous membranes, &c. The acini themselves do not become coloured under these circumstances ; nor is the bile coloured, which is secreted by them at the same time ; absorption in the liver does not, therefore, take place in the acini, but in the coarser gall-passages (Heidenhain).

It is uncertain from which of the two kinds of blood flowing into the liver the materials for the preparation of bile are chiefly derived. According to some investigators (Oré, Frerichs, and others), ligature or obliteration (Kottmeyer) of the hepatic artery suspends the secretion of bile, while that of the portal vein has no such result. Other researches (Schiff) have led to exactly opposite results. Natural injection of the portal vein with colouring matters colours the periphery only of the lobules, injection of the hepatic artery only the centre ; it is, therefore, probable that both sets of vessels are concerned in secretion (Chrzonszczewsky and Kühne). Comparative examinations of blood flowing into and out of the liver have merely approximately disclosed the nature of the substances which are retained in the liver and there converted into the constituents of bile. Analysis of blood from the portal and hepatic veins shows that, apart from the appearance of sugar in the latter (Chap. V.), hepatic venous blood contains less water, albumin, fibrin, fats, blood-colouring matter and salts,

but more blood corpuscles (Chap. V.) than portal blood, which, especially after digestion, is very rich in fats (Lehmann, C. Schmidt). The high temperature of the gland and of hepatic venous blood shows that active oxidation goes on during secretion.

Of the more special chemical changes which take place during secretion, the most probable is the formation of the biliary colouring matters from blood-colouring matter, which is based upon the identity (Virchow, Valentin, Jaffe), or at least the strong resemblance (Städeler and Holm) of bilirubin and hæmatoidin (p. 28). Some maintain, also, the origin of cholic acid and sugar from fats, the glycerin, according to various hypotheses, yielding sugar, and the fatty acids, cholic acid; but the existence of such processes is as yet unsupported by facts. The processes of decomposition which take place during digestion may possibly account for the origin of glycocine and taurine; and the further syntheses in which they take part may have their seat in the liver. The glycocine of the liver may be conjugated with other acids than cholic acid, *e.g.* with benzoic acid, to form hippuric acid (see under Urine).

The amount of bile secreted, which it is impossible to estimate exactly, varies between about 160 and 1,200 grms. in twenty-four hours (as Ludwig has estimated from the data of others). It depends to a large extent upon the food taken. It is increased by ingestion of water (in which case the bile is more watery), by an animal diet, and, to a less extent, by a vegetable diet also. Fatty foods do not at all increase the amount secreted; and starvation diminishes it considerably. The maximum of secretion is reached several hours after the ingestion of food, and it occurs the later the more plentiful the meal has been (Béchamp). What influence the nervous system may have upon the formation of bile is not yet known; from several experiments it would seem that irritation of the vaso-motor nerves of the liver diminishes secretion (Heidenhain).

Other substances may be found abnormally in the bile, which have been taken into the body along with the food, and are being voided by this way. Heavy metals, especially, are said to find their way into the liver and the bile. Copper and lead occur somewhat regularly in the liver.

Concerning other functions of the liver, see Chapter V.

Separation.

The out-flow from the liver of the bile already formed is occasioned probably by the mechanical pressure exerted by the

secretion, assisted by the compression of the liver during inspiration. The amount of bile collected from fistulæ is, therefore, diminished during the slow respiration after section of the vagi (Heidenhain). The evacuation of the gall-bladder and the larger gall-passages, however, is probably brought about by the contraction of their smooth muscular fibres, which takes place simultaneously with the movements of the intestine. By irritation of the spinal cord this evacuation can be artificially induced (Heidenhain).

As animals with biliary fistulæ quickly grow lean, provided they are prevented from devouring the bile which escapes, it is supposed that the greater portion of the bile is reabsorbed in the intestines. The ultimate destination of the reabsorbed biliary matters is, however, not known; nor have the other circumstances, which help to explain the starvation of the animals from which the biliary secretion is removed, been completely eliminated from the question. Moreover, in the normal condition, all the biliary substances are found in the fæces in considerable quantities—the colouring matters which colour the fæces, bile-acids, mucus, cholesterin, &c. The bile-acids, especially taurocholic acid, undergo in the lower part of the intestinal tube a hydrolytic decomposition (Chap. III.); there being found in the fæces, therefore, glycocholic acid, cholic acid, and their anhydrides, choloidic acid and dyslysin (Hoppe-Seyler). The reabsorption of the specific constituents of bile is, therefore, yet doubtful.

Unlike all the other secretions connected with the digestive apparatus, bile is probably of no importance in digestion proper (*i.e.* in the preparation of food for absorption). The one property it possesses, which is of value for that purpose, viz. that of emulsionising fats, is shared by it with other secretions which possess it in a far higher degree (pancreatic juice, and, perhaps, intestinal juice). Solutions of peptones are precipitated by bile (p. 99) ; a circumstance the importance of which will be spoken of in the next chapter. The importance of bile physiologically appears to be chiefly in regard to the absorption of fats (Chap. III.). Bile (and the salts of the bile-acids), for instance, renders possible both filtration of fats through membranes under slight pressure, and diffusion between fats and watery solutions (von Wistinghausen), probably because it oc-

casions the simultaneous imbibition of both (a condition of diffusion, p. 85) in the form of soapy solutions. It renders easier, also, the passage of fats through narrow. (capillary) tubes. Bile is also said to induce contraction of the muscular fibres of the villi (Chap. III.) (Schiff), and thus, again, to assist in the absorption of fats. It appears moreover to prevent putrefactive decomposition of the contents of the intestine.

In accordance with what has been said above, when bile is suffered to escape through a fistula, there occurs no essential disturbance of the digestive processes, but only (1) prevention of the absorption of fats (as indicated by the fat contained in the fæces, and the absence of fat in the chyle); (2) colourless, ill-odoured, hard fæces; (3) at the same time excessive hunger on the part of the animal: (4) the endeavour on the part of the animal to make up for the deficient absorption of fat by increased consumption of hydro-carbonaceous foods (Chapter VI.).

5. *Pancreatic Juice.*

The pancreatic juice secreted in the racemose pancreas, whose structure resembles closely that of the salivary glands, is a strongly alkaline, clear, very tough, colourless fluid, coagulable by heat. Its specific constituents are (1) several albuminous bodies coagulable by heat, which are scarcely distinguishable from albumin itself, and to which many observers ascribe the fermenting properties of the secretion (pancreatin). According to others (Danilewsky) the ferments of the pancreatic secretion are special bodies. (2.) Several hydrolytic ferments (see below) capable of separation one from another. (3.) Leucine and other products of decomposition of albuminous bodies.

Pancreatic juice may be obtained by means of artificial fistulæ; and an artificial juice may be made by infusing the glandular substance in water.

The pancreatic juice has, by virtue of the ferments it contains, three well-marked properties which render it very important in digestion: (1.) It converts starch-mucilage into dextrin and sugar more powerfully than saliva from the mouth (Bernard). (2.) It decomposes neutral fats very quickly, in such a manner that, in the presence of water, glycerin and free fatty acids are formed (p. 19); the latter then partly combine with the alkali of the pancreatic juice to form soaps, while the excess causes an acid reaction. With the decom-.

position is connected an emulsionisation of the fats (Bernard), which is probably brought about by the products of decomposition themselves (Brücke). (3.) Coagulated albuminous bodies are dissolved by the pancreatic juice, as also is gelatin (Corvisart). This solution takes place only when the fluid is alkaline (compare, on the contrary, the effect of gastric juice), and is not preceded (as in gastric juice) by a swelling-up, which even hinders the process (Danilewsky). The solution agrees in its properties with peptone-solutions (Kühne). After some time, however, the peptone is further split up with the production of leucine, tyrosine, and unknown extractives, of which one is coloured violet on the addition of chlorine, and another—indol—possesses a disagreeable fæcal odour (Kühne). These processes are not of the nature of putrefaction.

The leucine contained in the pancreatic juice is the result of the action of the juice upon its own albumin, as is also the substance which produces the red colouration of the pancreas when treated with chlorine (Tiedemann and Gmelin). Alkaline albuminate is digested by the pancreatic juice, though more slowly than fibrin (Senator): so also are gelatin and the gelatigenous tissues. It is remarkable that all the results of pancreatic digestion are such as may be produced by boiling with mineral acids (see p. 19). By injecting melted paraffin into the excretory duct the cooperation of the pancreas in digestion can be prevented, without the latter process being essentially disturbed (Schiff).

The pancreatic juice of the dog contains 91 per cent. of water, 8·2 per cent. of organic matter, 0·8 per cent. of ash (Bernard).

Secretion.

The secretion of pancreatic juice probably never takes place without nervous stimulation (as in that of saliva). It is usually very slight, but increases much during digestion. That the specific constituents of the secretion are formed in the glandular cells, is proved by (1) the activity of an infusion of the glandular substance, and (2) the presence of cell-fragments in the secretion (Donders). It may be assumed, therefore, that the constituents become free in this case also by the disintegration of the cells. Increased secretion is constantly accompanied by increased circulation, and reddening of the gland (Bernard). We may, therefore, suppose some vaso-motor effect of the nerves, as is the case with the salivary glands.

The nerves affecting this secretion are unknown; they appear to be called into action reflexly by stimulation of the gastric mucous membrane, just as are those of the salivary glands on stimulation of the mucous membrane of the mouth (Ludwig): hence the secretion of the gastric and pancreatic juices occurs simultaneously (Bidder and Schmidt). Irritation of the medulla oblongata increases the flow, probably only by inducing contraction of the duct (Landau). Irritation of the central end of the vagus stops the secretion (N. O. Bernstein); the same stoppage occurs during vomiting (Weinmann, Bernard). The relative amount of solid constituents is inversely proportional to the rapidity of secretion (Weinmann); that of salts, however, is pretty constant, and is the same as in blood-serum (N. O. Bernstein).

The quantity of pancreatic juice secreted cannot be accurately estimated by means of fistulæ, because the pancreas has two anastomosing excretory ducts. The ultimate destination of the secretion is probably the same as that of saliva and gastric juice.

6. *Intestinal Juice.*

Intestinal juice (Succus entericus) is the secretion poured out by the tubular glands of Lieberkühn, which are present in all parts of the intestine. (The racemose glands of Brunner in the duodenum resemble in construction the pancreas; their secretion is, according to recent observations, most like mucus). It was not possible until quite recently to obtain pure intestinal juice. The method now adopted is as follows (Thiry): An animal is taken and a portion of the intestine, still connected with the mesentery, is separated from the rest. The two ends of the remaining portion are made to unite, the animal continuing to live, but with an intestine somewhat shortened. The portion separated from the rest is closed at one extremity, while the other is stitched to the sides of the wound in the abdomen. As the nutrition of the piece of intestine has not been interfered with, secretion will take place as usual, and the intestinal juice will be poured out at the open end.

The juice so obtained is a thin, bright yellow, strongly alkaline, albuminous fluid. It acts as a ferment only on fibrin, which it quickly dissolves (it does not dissolve other coagulated albuminous bodies, Thiry). Nothing is certainly known concerning the chemical constituents.

Under ordinary circumstances secretion is almost quiescent; but under the stimulation of mechanical irritation or weak acids,

it may be largely increased (13 to 18 grms. hourly from a surface of 100 sq. cm.)

Formerly an impure intestinal juice was obtained through intestinal fistulæ by the removal of the food, or by introducing sponges into the intestine, or by preventing the admixture of the other secretions which are poured into the intestine. According to an older view, which has been supported in part in recent times, intestinal juice acts upon starch (Schiff, Quincke), and upon fats (Schiff), like the pancreatic secretion, but somewhat more slowly. The ferments extracted from the intestinal mucous membrane by means of glycerin do not possess the power of digesting albumin, although they can convert starch into sugar. The glands of the large intestine are unable to bring about the latter operation (Eichhorst, Costa).

The intestinal juice of the dog contains 97·6 per cent. of water, 0·8 per cent. of albumin, 0·7 per cent. of other organic matters, 0·9 per cent. of ash (Thiry).

2. Respiratory Secretions.

The lungs may be regarded in structure and function as a racemose gland with a gaseous secretion, the excretory duct of which is the trachea. As will be explained in Chap. IV., the forces which effect the separation of carbonic acid at the lungs are by no means thoroughly understood.

The numerous mucous glands which are scattered about the air passages, from the nasal opening in the face to the smaller bronchial tubes, yield a fluid mucus. The glands are racemose and possess pavement-epithelium; the smallest of them are, however, more tubular, and are provided with cylindrical epithelium. The same remarks apply to this secretion as to that of the mucous glands of the alimentary apparatus (p. 92). The mucus is apparently secreted only in small quantities, and the excess is removed from the body by an arrangement which will be spoken of hereafter (Chap. IV.)

3. Urinary Secretion.

The urine secreted in the kidneys is a true excretion, the removal of which from the organism is necessary, as it is of no further use (p. 83, ' Excretions'). It serves to carry out of the body certain ultimate products of the oxidation of nitrogenous substances, as well as the excess of water. The products of oxidation are separated along with salts in the form of watery solutions.

The long-pending question as to whether these ultimate results of oxidation exist as such in the blood and are merely separated in the kidneys; or whether some of them remain until they reach the kidneys in a partially incomplete form, and ought, therefore, to be considered in the light of ' specific constituents' of the urinary secretion; has not yet been decided (see below).

Urine is a clear, transparent, amber-coloured and slightly acid fluid, with a bitter saline taste and an aromatic odour (specific gravity 1·005—1·030). A little mucus from the mucous glands of the excretory ducts (especially of the bladder) is usually mixed with it. Its specific constituents[1] are :—1. Urea, the chief ultimate product of the oxidation of nitrogenous bodies, part of which is pre-formed in the blood, but some of which does not, in all probability, appear until the kidney is reached. 2. Uric acid, a less oxidized product, existing in the form of neutral urates of the alkalies. 3. A series of still less oxidized bodies, which occur for the most part in small quantities, and some (those marked with an asterisk) only occasionally :— * Allantoine, xanthine, hypoxanthine (sarcine), creatinine, glycocine (only, however, conjugated with benzoic acid in the form of hippuric acid), *taurine, *cystine, *leucine, *tyrosine, ammonia, both free and in the form of salts (amongst others, in the form of ammonium oxalurate (p. 23), Neubauer). 4. One or more colouring matters (urobilin, urohæmatin, &c., see p. 29), besides indican. 5. Certain unknown bodies, so-called extractives (*e.g.* that which occasions the odour). The remaining constituents of urine are : 1. Water. 2. Salts (the usual blood-salts; but, in addition, some which are also probably oxidation-products, *e.g.* oxalates and sulphates produced possibly by the oxidation of bodies, especially taurine, containing sulphur). 3. Small quantities of sugar (Brücke). 4. Gases : oxygen, nitrogen (a remarkably large amount, Morin, Pflüger), carbonic acid.

The colour of urine varies with its state of concentration: it is darkest in the concentrated morning-urine (' urina sanguinis'), and lightest in that passed after the plentiful ingestion of fluids (' urina potus.') The acid reaction results for the most part from the contained acid sodium phosphate (Liebig). That urine contains no free acid is proved by the fact that it gives no precipitate on the addition of sodium hyposulphite (Huppert). Sometimes normal urine is alkaline, namely, after caustic alkalis, or alkaline

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[1] Note what was said in the paragraph above.

carbonates, or salts of vegetable acids have been taken into the stomach. (The latter, viz. the salts of the vegetable acids, having undergone oxidation, appear in the urine as carbonates, which have an alkaline reaction, Wöhler).

On standing, urine forms gradually a precipitate of acid urates or free uric acid. Simple cooling cannot be the cause of this, for, on again heating to the temperature of the body, the sediment is not completely redissolved. We must, therefore, suppose an acid-formation to take place, by a species of fermentation, due probably to the influence of the mucus which is present ('acid fermentation,' Scherer). After some time (which is shorter the higher the temperature) decomposition sets in, owing to the organic germs which the urine receives from the atmosphere; in this process urea is converted into ammonium carbonate, the reaction becomes alkaline (' alkaline fermentation '), a putrefactive odour appears, and precipitates of ammonium urate, ammonio-magnesium phosphate, &c., are formed, with the development of fungi and infusorians.

Which of the above-mentioned specific constituents of urine are most extensively represented seems to depend upon the kind of food taken. In flesh-eating mammalia, such as man, urea is present in largest amount; very little uric acid and hippuric acid are found. In the urine of vegetable-feeders, but little urea and no uric acid are present, while hippuric acid abounds. Dietary changes effect variations in the urine. Among the exceptional bodies found in urine are hyposulphurous acid (Schmiedeberg) in the urine of animal-feeders, and carbolic acid (Städeler) in that of vegetable-feeders. The latter in all probability results from the action of acids upon some complex aromatic body (perhaps indican or hippuric acid)(Hoppe-Seyler and Buliginski). Succinic acid, which was described (Meissner) as a constituent of the urine of men and animals, is at any rate not found constantly (Salkowski). Human urine also varies with the food ingested (see below), hippuric acid, especially, increasing with the increase of vegetable food taken, and disappearing when animal food alone is eaten. The urine of birds, scaled amphibia, insects, &c., which becomes solid immediately after evacuation, contains, on the contrary, an excess of uric acid or urates; that of birds contains also urea, creatine, albumin, &c. (Meissner).

Numerous substances taken into the body as foods or medicines reappear partly unaltered in the urine, *e.g.* most metallic salts, alkaloids, colouring matters, alcohols. Other bodies appear in a more oxidized form. Especially is this the case with the alkaline salts of many organic acids (lactic, succinic, acetic, citric, and malic acids), which appear as alkaline carbonates and render the urine alkaline (Wöhler); and with benzol, which is found again in the form of carbolic acid (Schultzen and Naunyn). Substances capable of complete combustion, such as glycerin, do not cause the appearance of special constituents in the urine. Many conjugate bodies suffer partial combustion; tannic acid, for example (the glucoside of gallic acid), yields gallic acid. Benzoic acid and several allied bodies, essential oil of bitter almonds, cinnamic acid, and chinovic acid yield by conjugation with glycocine, hippuric acid (Wöhler); similarly some substitution-derivatives of benzoic acid (chloro-benzoic acid, nitro-benzoic, salicylic, and anisic acids),

coupling themselves with glycocine, give rise to corresponding hippuric acids.

The simpler amido-acids, glycocine and leucine, reappear as urea in urine (Schultzen and Nencki). Sarcosine, on the contrary (p. 26), unites with carbamic acid (p. 22), water being eliminated, and appears as sarcosine-carbamic acid ($C_4H_8N_2O_3$) in the urine (Schultzen); a part unites in a similar manner with sulphamic acid ($NH_2 \cdot SO_2 \cdot OH$), and appears as sarcosine-sulphamic acid ($C_3H_8N_2SO_4$). In like manner, taurine appears in the urine united with carbamic acid, as taurine-carbamic acid ($C_3H_8N_2SO_4$) (Salkowski).

$$H_2N—CO—OH \qquad H_2N—CO—N{<}^{CH_3}_{CH_2}{—CO—OH}$$
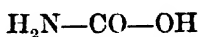
Carbamic acid   Sarcosine-carbamic acid

$$H_2N—SO_2—N{<}^{CH_3}_{CH_2}{—CO—OH}$$
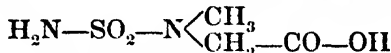
Sarcosine-sulphamic acid

The hippuric acid in the urine of vegetable-feeders is formed most probably out of some vegetable substance resembling benzoic acid taken into the body as food; the glycocine necessary for its formation is derived from the liver (Kühne and Hallwachs). The vegetable substance is probably the cuticular substance of plants which appears most to resemble chinovic acid in composition (Meissner and Shepard): for those portions of plants which possess no cuticular substance (*e.g.* underground portions, huskless grains of corn), yield no hippuric acid. It is, however, possible that other similarly occurring substances, which are allied to benzol, are the source of the hippuric acid (Nencki).

The following numbers represent the average composition of urine, which, however, is very variable. In 1,000 parts: Water 960, urea 23·3, uric acid 0·5, sodium chloride 11·0, phosphoric acid 2·3, sulphuric acid 1·3, ammonia 0·4 (Vogel).

Secretion.

The secreting apparatus of the kidneys (for a more detailed account of the structure of which refer to Manuals of Histology) consists of the *tubuli uriniferi* and the *vessels* connected with them. Every uriniferous tube ends in the cortical portion of the kidney in a globular dilatation called a *capsule* or *Malpighian body*, containing a *glomerulus*. The glomerulus is a small coil of vessels, produced by the branching and re-uniting of the finest twigs of the renal artery (vas afferens). The vessel formed by the reunion of the branches of the glomerulus (vas efferens), on emerging from the Malpighian body, again divides up into true capillaries, which intertwine with the tubuli uriniferi, especially with their convoluted commencements, and finally unite with the initial branches of the renal vein.

As the blood in the glomeruli is subjected to a high pressure on account of the resistance of the second capillary system in front, a free filtration into the capsule must take place. Water and those constituents of the blood which form true solutions (salts, urea, sugar, &c.) will, therefore, pass into the tubuli uriniferi. Albumin, &c., which do not form true solutions, do not filter through except under an abnormally increased pressure (p. 85). The very dilute solution thus formed now comes into proximity, at the walls of the tubuli uriniferi, with the blood which it has just left, and which is in a concentrated state owing to the loss of water; diffusion must result (Ludwig), leading to a return of water into the blood, and to a consequent concentration of the urine. Besides these physical processes, other causes seem to co-operate in the formation of urine. Many circumstances lead us to suppose that the glandular cells (epithelium) especially assist ; pathological degeneration of the epithelial cells, for example, interferes with secretion ; and, in birds, uric acid deposits are seen to originate within the cells, the disintegration of which seems necessary before the deposits can become free (von Wittich, Meissner).

As the branches of the vas afferens lie at the periphery of the glomerulus, while the vas efferens proceeds from its centre, the flow of blood from the former into the latter is rendered easy. Any tendency to a *return* of the blood would, however, be hindered ; for an increase of pressure in the branches of the vas efferens must force the branches of the vas afferens against the walls of the capsule and close them (Ludwig).

The part played by the kidney-substance in the formation of urine is regarded by some authors simply as a peculiar attraction exerted by its cells for the small quantities of urea or uric acid of the blood (Bowman). Many do not consider the small amounts of these bodies contained in the blood to be any objection to this, purely physical, theory of secretion ; for (they urge) the swiftness of the blood-stream through the kidneys is sufficient to account for the amounts secreted. Other observers, on the contrary, suppose that the formation of urea, uric acid, &c., from less oxidized bodies, takes place within the kidneys (Hoppe-Seyler and Oppler, Hoppe-Seyler and Zalesky). The facts, however, upon which this theory is based, are doubted or otherwise explained by others (Meissner, Voit).

The following are the points which are chiefly contested : (1.) The simple question whether the blood of the renal artery contains more urea than that of the renal vein (Picard), appears to have been recently settled in the affirmative (Gréhant) ; this difference disappears after ligaturing the ureters. (2.) According to some observers (Bernard and Barreswil, Oppler, Zalesky), after extirpation of the kidneys or ligature of the renal vessels,

no accumulation of urea takes place in the blood; while others (Meissner, Voit, Gréhant), maintain that such an accumulation may be detected, some even affirming that it varies in amount according to the time (Gréhant). If the former account be correct, it is still no proof of the formation of urea in the kidneys; for, after the operation, fluids containing urea and ammonia are vicariously secreted by the stomach and intestine, and are got rid of by vomiting (Bernard and Barreswil). Moreover the animals die for the most part so quickly (of so-called 'uræmia,' whatever that may be—whether the retention in the body of some poisonous substance, or simply of water), that no considerable accumulation of urea is possible, such, *e.g.* as that which follows simple ligature of the ureters. Extirpation of one kidney does not diminish the amount of urea excreted (Rosenstein). (3.) The presence in the kidneys of characteristic bodies which do not pass into the urine (*e.g.* cystine, taurine), certainly indicates the occurrence of processes of change in the kidneys; but it does not directly prove the formation of urea or uric acid there. (4.) The accumulation of creatine, creatinine, &c., in many organs (in blood, muscles), after extirpation of the kidneys (Oppler, Zalesky), is explained by the supposition that urea is normally derived from them in the kidneys. Creatine, again, is said to undergo conversion into urea on digestion with triturated kidney substance (Ssubotin). As, however, creatine and creatinine, when administered, reappear, as a rule, in the urine, unaltered, and not as urea (Meissner, Voit), it would seem, that these substances are not in general the source of the urea. In the present state of our knowledge, therefore, we must incline to the belief that urea and uric acid are separated from the blood and not formed in the kidneys.

In birds and serpents, ligature of the ureters is followed by an evident accumulation of uric acid all over the body. After extirpation of the kidneys in serpents,[1] there is simply a diminution in the amount of uric acid excreted (Zalesky), which produces no decided effect.

If we then assume that the two essential constituents of urine reach the kidneys already formed, the liver may possibly be one of the principal situations for their production; for, of all organs, it contains most urea, or (in the case of birds) uric acid (Heynsius, Stokvis, Meissner): and it yields urea to blood which is passed through its vessels (Cyon, Gscheidlen).

Besides the above-mentioned circumstances affecting the secretion of urine, the following conditions influence the amount secreted in a given time, and the substances contained: 1. The quantity of urine depends (*a*) upon the intensity of the blood-pressure in the glomeruli; (*b*) upon the amount of materials of an easily diffusible nature (water, salts, &c.) contained in the blood. This is evident, for the greater the blood-pressure the larger will be the amount filtered in a unit of time, and the greater the amount of water, salt, &c. in the blood

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[1] In birds, in consequence of the situation of the kidneys, they cannot be extirpated without killing the animal.

the less will be the amount of the filtered substances which will re-diffuse into the blood-vessels from the tubuli uriniferi; and, therefore, the greater will be in both cases the quantity of urine secreted. Among the circumstances which raise the blood-pressure in the glomeruli must be reckoned: 1. Rise of blood-pressure all over the body, as when the distension of the vascular system is increased (*e.g.* by a free ingestion of water, which is quickly absorbed); 2. Increased tension of the arterial system alone, produced by excessive activity of the heart; 3. Increased tension in the renal arteries produced, for example, by ligaturing other great arteries; or simply in the glomeruli owing to a vaso-motor dilatation of the vasa afferentia; 4. Prevention of the free outflow of blood from the glomeruli through the veins (*e.g.* by the morbid contraction of the capillaries, or the ligature of the renal veins). Any very decided increase of pressure, especially when produced by the 4th of the above methods, causes, in addition, a filtration of the less diffusible portions of the blood—albumin, fibrinogen—into the urine; and an increase above a certain limit leads to the appearance in it of blood (blood-corpuscles), owing to the rupture of the vessels, or, perhaps, to diapedesis (p. 81). Circumstances of a nature opposite to those we have mentioned above—especially, therefore, diminished tension of the arterial system, occasioned, for example, by diminished cardiac activity (heart-diseases)—must cause the amount of urine secreted to diminish. Among the substances of an easily diffusible nature referred to above, the water contained in the blood will have the greatest influence upon the amount of the urinary secretion: as a fact, the quantity secreted depends chiefly upon it, and therefore, as is explained above, upon the water ingested. The amount of each individual constituent of the urine depends (*a*) upon the amount of it previously contained in the blood and possibly also (*b*) upon the oxidizing power of the kidneys. The following may be increased: 1. The water by ingestion (drinking), and by diminishing secretion in other ways, as by perspiring and expiring under a low temperature. 2. The salts, by an increased use of salts in food (certain salts which are formed in the body by oxidation, of course, increase with the extent of oxidation). 3. The sugar, by an increased formation of sugar in the liver, or by a diminished destruction of what is formed

(Chapter V.). 4. The products of the oxidation of nitrogenous bodies (considered as a whole and not as individual bodies—urea, uric acid, creatinine, &c.), by an increase in the amount of the nitrogenous foods, such as flesh, eggs, &c., which are assimilated ; and also by an increased destruction of substances in the body containing nitrogen (as in excessive nervous activity, abnormally high temperatures, fever, &c., Chapter VI.). 5. The carbonic acid, by an increase in the number of operations, especially of muscular movements (Morin), which generate carbonic acid in the body.

From what has been said above it is easy to collect and mention all the circumstances which increase the quantity of urea excreted in a given time. They are (1) general increase in the urinary secretion, from whatever cause resulting ; (2) free ingestion of animal food ; (3) increased consumption in the body of nitrogenous material (see Chapter VII. and Chapter VIII.) ; and (which is doubtful) (4) increased power of oxidation on the part of the kidneys.

Besides the substances we have mentioned, there may be detected in the urine, after certain foreign bodies have been taken into the system, either those bodies themselves or some oxidized modification of them. The urinary secretion brings about a constant elimination of them from the body. In the case of poisonous substances, if elimination takes place as quickly as introduction into the blood, e.g. when absorption is taking place from the stomach, a complete immunity from danger may result. Certain easily diffusible poisons, therefore, such as curare, are harmless when taken into the stomach during a constant secretion of urine. When injected directly into the blood, or when quickly absorbed (as in subcutaneous injections), or if the activity of the kidneys is interfered with by ligature of the renal vessels (Bernard, Hermann), they act at once as poisons. As it is possible that we frequently take into the body along with food many harmful substances of this nature, their elimination at the kidneys is a further important function of those organs.

The quantity of urine excreted in twenty-four hours varies in adults (chiefly on account of the fluid ingested), between 1000 and 2000 grammes ; the amount of urea is on the average 30 grammes, of uric acid 1 gramme, and of hippuric acid 1–2 grammes.

That the nervous system has some influence upon the secretion of the kidneys, is proved by the changes which take place in the urine referable to emotions and to nervous diseases. From the statements we possess respecting the nature of this influence, but which are not very exact (Bernard, Eckhard,

Knoll, Ustimowitsch), it would seem to be chiefly vaso-motor. Section of the nerves accompanying the renal vessels, as also of the splanchnics and of the cord, as well as lesion of a certain portion of the fourth ventricle of the brain, increase the secretion as a rule. At the same time the renal veins pulsate, the blood in them usually becoming bright carmine-red in colour, on account of the rapid flow from the arteries. Irritation of the splanchnics diminishes the secretion and the rapidity of the blood-stream through the kidneys.

Irritation of the vagus, on the other hand, is said to have an opposite effect, viz., to increase the secretion and the rapidity of the blood-stream (Bernard) ; and therefore, like the fibres of the facialis to the salivary glands (p. 95), to dilate the arteries. The result of section of vaso-motor nerves is the less certain the greater the number of fibres severed. If, for example, the splanchnics or the upper part of the spinal cord be cut through, the general arterial pressure sinks to such an extent that the dilatation of the renal arteries is more than balanced. After section of the renal nerves the gland undergoes change, and the urine secreted becomes albuminous (Krimer, Brachet, Müller, and Peipers).

Separation.

The urine after secretion passes out of the convoluted into the straight uriniferous tubes, which unite several times at acute angles one with another, and open, at the surface of the renal papillæ, into the calyx or pelvis of the kidney. In all these situations urine is constantly found ; a return of the secretion from the pelvis into the tubuli is impossible, as any increase of pressure in the former closes the openings of the latter. From the pelves of the two kidneys the urine passes through the ureters (one to each kidney) into a reservoir—the urinary bladder. The passage through the ureters may be accounted for by (1) the pressure exerted by the continually secreted urine ; (2) the weight of the contained secretion (for the bladder is, in almost every position of the body, lower than the kidneys); (3) peristaltic contraction of the muscles of the ureters, which, it would seem, propels every drop of the fluid reaching the ureters by continually closing the lumen of the tube behind it. The urine collects in the bladder (which, when empty, is collapsed in folds), until it completely fills out the walls of that organ ; every further addition then causes an abnormal distention. The return of the urine into the ureters is prevented

by the peculiar arrangement of their openings, which traverse the walls of the bladder very obliquely, in such a manner that pressure from within closes the channel entirely. The passage of the stored-up secretion into the urethra is controlled by a ring of elastic fibres; and, in males, by the elasticity of the prostate also. As soon as the pressure of the urine overcomes the elasticity of those structures, and a drop of urine trickles into the urethra, an impulse to micturition is felt; whereupon either the closure of the neck of the bladder is rendered firmer by the voluntary contraction of the urethral muscles (Budge), or a voluntary evacuation of the contents of the bladder is commenced. The latter is accomplished by the contraction of the muscular walls of the bladder which proceeds gradually until the lumen of the bladder is completely obliterated, and the whole of the contents are expelled. The urethra itself is next emptied by means of the muscles surrounding it (especially by the bulbo-cavernous muscle). The evacuation of the contents of the bladder is assisted by abdominal pressure (Chapter IV.).

During its stay in the bladder the urine is said by some to lose a portion of its water by absorption (Kaupp); while others, on the contrary, maintain that it receives a further addition of water from the blood, at the same time yielding up to the latter some of its urea (Treskin); and a third set of observers deny that any diffusion whatever takes place, as the bladder is unable to absorb solutions of salts so long as its epithelium is intact (Küss, Susini). Mucus from the numerous mucous glands is mixed with the urine both in the bladder and in the urethra.

The peristaltic movements of the ureter are reflex in their character, as they only occur on stimulation of the ureter by the urine forced into it, or on artificial irritation: they proceed in the direction of the bladder with a rapidity in rabbits of 20 to 30^{mm} per second (Engelmann). Each individual irritation of the ureter produces a wave of contraction on both sides of the point of irritation; as this may take place in portions of the ureter containing no ganglia or nerves, the wave of movement would seem to be continued by simple muscular conduction. The spontaneous movement of the ureter has been recently regarded as a case of automatic contraction of muscle (Chapter VIII.) (Engelmann).

The above theory of the closure of the bladder is disputed by some, who suppose that it is produced by a sphincter, kept constantly in a condition of contraction (tonus) by the nervous system (Heidenhain and Colberg, Sauer, Rosenplatner, Kupressow). The presence of this sphincter in man is denied by some (Barkow), but maintained by others (Heidenhain); while the existence of a constant tonus has been contested on experimental grounds (L. Rosenthal and von Wittich).

The nerves of the muscles of the bladder, according to some, may be

traced into the cord (lower portion, Budge), and even into the brain (Kilian, Valentin). They can be brought into reflex action very easily by stimulations originating in the mucous membrane of the bladder, and in the bulbus urethræ. Over-distension of the bladder, therefore, causes involuntary evacuation of its contents.

Retention of urine produced by paralysis of the muscular walls of the bladder frequently follows degeneration of the spinal cord (Chapter XI. Spinal Cord).

4. CUTANEOUS SECRETIONS.

Concerning the respiratory secretion of the skin, see Chapter IV.

1. *Sweat.*

Sweat is the secretion of the numerous tubular sweat-glands of the skin, the inner, blind, extremities of which are coiled up, and lie for the most part in the corium, but sometimes in the subcutaneous layer of connective tissue, while their outer, free, extremities open at the surface as the ' pores ' of the skin.

The sudoriparous secretion conveys out of the body the same excretory matters, generally speaking, as the urine, from which it is chiefly distinguished by the facts that it is not constantly secreted, and that it is poured out over the whole skin, and is of further use to the organism as a regulator of temperature. [The sweat-glands, therefore, bear the same morphological relationship to the kidneys as the mucous glands to the salivary glands, the glands of Brunner to the pancreas, or the sebaceous glands to the milk-glands.]

Sweat in large quantities may be obtained by supporting the body on an inclined grooved plate of metal and submitting it to a vapour bath; or by covering portions of the body with air-tight bags connected with a receiver. Sweat so obtained is almost always rendered impure by the presence of sebaceous secretion and epithelium-scales.

Sweat is apparently a colourless, clear, acid fluid of variable odour according to the part of the skin whence it was taken. The constituents of sweat are : 1. Water; 2. The usual salts; 3. Urea (and perhaps other products of the oxidation of nitrogenous bodies—Favre, for instance, mentioning an acid containing nitrogen, hidrotic acid); 4. Traces of a colouring matter (Schottin); 5. Fats; 6. Various volatile fatty acids (formic, acetic, butyric, propionic acids, &c.).

Fats predominate in the secretion of the sweat-glands of the external ear (ceruminous glands) to such an extent that it resembles rather a

sebaceous than a sudoriparous secretion. Sweat is easily decomposed; and decomposition may chiefly affect its fatty portions, in which case the odour of the volatile acids and the acid reaction increase; or it may chiefly affect its nitrogenous portions, when ammonia appears and the secretion takes an alkaline reaction.

The quantitative composition of sweat is about the following (in 1,000 parts): water 995·6, urea 0·04, fats 0·01, other organic matters 1·88, inorganic matters, 2·5 (Favre).

Secretion.

The secretion of sweat only takes place under certain conditions. It consists most probably in part of a process of transudation, and in part of a peculiar activity of glandular cells. The fat at least, contained in the secretion, originates in the cells; for the latter contain fat-globules, and in greater quantity the richer the secretion is in fats or fatty acids. Secretion is promoted by various circumstances : 1. By whatever raises the blood-pressure in the capillaries of the sweatglands as, a, general rise of blood-pressure (*e.g.* after free ingestion of water); b, increase in the temperature of the body, or in the vicinity of the body, which causes dilatation of the afferent arteries (possibly by relaxing their muscles). In such circumstances the secretion of sweat is of special importance; for the evaporation of the secretion extracts heat from the body and cools it (Chapter VII.). 2. By increase in the quantity of the various constituents of sweat contained in the blood, and especially of water. Liberal ingestion of warm fluids, therefore, increases perspiration for several reasons. To what extent the above-mentioned influences must operate in order to induce ordinary secretion is unknown. The quantity secreted, of course, varies very much. Frequently no perspiration takes place for months; while, at other times, as much as 1600 grammes and more are yielded in an hour (Favre). Those portions of the skin (the forehead, the axillæ, the soles of the feet, and the palms of the hand, &c.) which are provided with many large sweat-glands, yield the richest supply of secretion. The value of the sweat to the whole organism is discussed in Chapters V. and VII.

It is probable that the nervous system has some influence upon the formation of sweat from the known effect which the emotions exert upon it. Nothing is, however, known of the way in which it operates; nor indeed,

have nerves been traced to the glands. We can, therefore, at present only admit the existence of vaso-motor influences. As is the case with the urine, substances taken into the body as food may pass into the sudoriparous secretion unchanged or oxidized. Hippuric acid is said to appear in the sweat, as well as in the urine, after ingestion of benzoic acid (Meissner). Indican also was once detected in sweat (Bizio).

2. *Sebaceous Secretion.*

The small, racemose, sebaceous glands of the skin open nearly always into hair-follicles; but the follicles are in many places so small as to appear to be simply lateral involutions of the excretory duct of the gland. The chief constituents of the sebaceous secretion are various fats, normally fluid at the temperature of the body, and cholesterin; in addition, there are found small quantities of the usual results of transudation (water, salts), and an albuminous body. It is supposed that, in secretion the specific constituents (fats) arise within the gland-cells, and become free by the disintegration of the latter. Possibly the liberation of the fat-globules is due to a process of contraction similar to that which takes place in milk. The cells of the more superficial layers in the gland-cavity may be seen to contain increasing quantities of fat ('fatty degeneration'), the most superficial being completely filled. The latter then disintegrate; and hence the secretion contains fragments of cells. An influence of the nervous system upon this secretion has not been demonstrated. The secretion lubricates the hair and also the skin, giving them a shiny appearance, and preventing the entrance of fluids.

Exact experiments with this secretion, especially of a quantitative description, are wanting, as there are no means of procuring large amounts of it except in the case of that covering the skin of new-born animals (vernix caseosa). The secretion of the Meibomian glands of the eyelids probably resembles the sebaceous secretion. Cerumen, on the contrary, is a secretion of sweat-glands, although there are sebaceous glands in the hair follicles of the external meatus.

The sebaceous secretion is closely allied to the following secretion—milk.

5. SECRETION OF MILK.

The milk-glands may be regarded as greatly enlarged and aggregated sebaceous glands, and the milk which they secrete

as a sebaceous secretion containing a greater quantity than usual of the results of transudation.

Each gland consists of 15–24 incompletely separated racemose glands, every one of which is provided with an excretory duct, which, after dilating into a longish reservoir, opens upon the nipple. These glands are only fully developed in the female during the period of possible fertility, and they are only active from about the period of delivery until the recurrence of menstruation.

A secretion of milk takes place in new-born children, from the fourth to the eighth day ; and also occasionally in males.

Milk is an opaque, white fluid, generally weakly alkaline, but frequently neutral or slightly acid (according to Soxlet the normal reaction is amphichromatic). It has a sweetish taste and a characteristic odour. It is an emulsion of very small fat-globules (milk-corpuscles) in a clear fluid. Its specific gravity is 1·008–1·014.

Casein also (see below) seems to belong to the list of formed elements of milk, as it does not appear in the clear filtrate obtained by filtering milk through clay by means of the air-pump (Zahn, Kehrer). It is probably contained in the fragments of cells present in the secretion (Kehrer). Many observers believe that the fat-globules possess an envelope of casein.

The constituents of milk are : 1. Water, in the proportion on an average of about 89 per cent. 2. Salts, especially compounds of potassium, calcium, and phosphoric acid, and also of iron and manganese, the combination of the saline constituents showing a striking resemblance to that in the blood-corpuscles. 3. Milk-sugar. 4. Albuminous matters, especially casein, but also a small amount of albumin ; that is to say, albuminous matters, only a small portion of which is precipitable by heat, the greater part being thrown down only on the addition of an acid. 5. Fats, viz. the glyceric ethers of palmitic, stearic and oleic acids, and in small quantities also of butyric, capronic, caprinic, caprylic and myristic acids. 6. Lecithin or protagon (Tolmatscheff). 7. Various 'extractives,' among others urea (Lefort). 8. Gases (CO_2,O,N).

Human milk contains in 1,000 parts (Th. Brunner): water 900·0, casein together with albumin (traces) 6·3, fats 17·3, milk-sugar 62·3, salts and

extractives 14·1. The milk of the cow contains (Kühn): water 885·3, casein and albumin 28·5, fats 31·2, milk-sugar 45·6, salts and extractives 9·8. Older analyses differ considerably from those here given.

Secretion.

The secretion of milk consists probably in the formation within the glandular cells of the specific constituents (milk-sugar, casein, and fat) out of the materials transuded through the walls of the blood-vessels, and the liberation of those constituents by the disintegration, or some similar process, of the cell-walls. In the case of the fat, this has been directly shown to occur, the innermost layers of cells having been observed to become more and more nearly filled with fat, in the same manner as in the sebaceous secretion. These fat-laden cells then either disintegrate, or, more probably (Stricker, Schwarz), get rid of their fat-globules by contracting, like colostrum-corpuscles to be described below. The globules thus set free become emulsionized in the fluid. The milk-corpuscles, as is generally the case with fat-globules found in albuminous fluids, become coated over with a thin pellicle of some alkali-albuminate (possibly casein). At the commencement of the period of lactation, in the so-called colostrum, or milk first secreted after delivery, certain round, unbroken, fat-laden cells (colostrum-corpuscles) present themselves. At first they are the only bodies present; but after a time they are replaced to a greater and greater extent, though never entirely, by the ordinary milk-corpuscles. It has been observed that the colostrum-corpuscles are contractile (Stricker, Schwarz), and force out their contained fat-globules; it may, therefore, be assumed that the subsequent formation of milk-corpuscles happens in like manner; and that it is only at first that the parent-cells of the milk-corpuscles themselves become free and pass into the milk. From which of the substances composing the transuded fluid the various specific constituents of milk are derived is still a matter of supposition. Casein undoubtedly originates in the albumin of the blood, as a ferment has recently been discovered in the milk-gland, which is capable of converting a mixture of albumin and an alkali into an alkali-albuminate (Dähnhardt). Milk-sugar is derived in all probability from the grape-sugar of the blood, as it is increased in quantity by the ingestion of

carbo-hydrates as food ; there are, however, other possible sources (Chapter VI.).

The origin of the fat is as doubtful as the method of the formation of fat generally (consult Chapter VI., where this question is discussed); some have supposed it to be derived from alkali-albuminates such as casein (Hoppe). The process of secretion is, therefore, as yet quite uncertain ; even the amount of salts contained in the milk cannot be accounted for on mere physical grounds. An influence of the nervous system, such as may and doubtless does exist, does not however seem indispensable for simple secretion, which continues after section of the cerebro-spinal nerves (in man the 4th to 6th intercostal nerves) and also of the nerves (sympathetic ?) which accompany the vessels in the gland (Eckhard).

Of the special circumstances affecting the secretion, those of diet are best understood. The amount of casein and fat present during an animal diet is greater than during a vegetable diet. A liberal supply of food generally causes increase in the amount of fat, while carbo-hydrates cause increase in the amount of sugar. Fatty foods do not increase the quantity of fat. The composition varies also with the time during which active secretion has proceeded, and with other circumstances attendant upon child-bearing.

As was the case with urine, milk may contain foreign bodies (in a changed or unchanged condition) which have been previously taken into the system.

As milk contains several easily alterable constituents, and, in all probability, some ferments also, it rapidly undergoes certain changes after its secretion, which may in part be artificially induced and utilised. The ferments may be partly separated by causing milk to transude through a membrane, when they are left behind (F. Hoppe). Certain of these changes may be proved to be processes of oxidation, and are accompanied by the disappearance of oxygen and the formation of carbonic acid (Hoppe). In the first place the milk-corpuscles, which are lighter on account of the fat they contain, rise to the surface of the milk on standing, constituting the ' cream.' By means of shaking (churning), the envelopes or pellicles of the milk-corpuscles, become ruptured, and in consequence the fat contained in them runs together, the fatty part of milk being thus obtained almost pure in the form of ' butter.' The remaining solution of casein, sugar, and salts, constitutes ' butter-milk ': as a rule, butter is manufactured by churning cream alone. Among the chemical changes occurring in milk the chief are those affecting the milk-sugar and the fats. The former gradually undergoes lactic acid fermentation, especially if the temperature be somewhat high, the milk becomes acid, and the free lactic acid precipitates

the dissolved casein, causing flocculence, just like any other free acid or like the gastric juice. This coagulum, 'cheese,' includes also other of the constituents of milk, especially the milk-corpuscles. The remaining solution of sugar and salts is called 'whey.' A formation of lactic acid frequently takes place while the milk is still within the gland, the secretion having an acid reaction as soon as it is withdrawn. No oxygen is needed in the formation of lactic acid (Hoppe). On the addition of yeast, milk may, under certain circumstances (probably such as cause the conversion of the milk-sugar into lactose), undergo alcoholic fermentation; such an alcoholic preparation of milk is the 'kumiss' of the Tartars. The fats also decompose, if milk or butter be allowed to stand, into glycerin and fatty acids (caprylic, caprinic, capronic, butyric acids). Moreover, milk on standing exposed to the air, exhibits a diminution in the quantity of casein, and an increase in the amount of the substances capable of being extracted by means of alcohol and ether. This is accompanied by absorption of oxygen and liberation of carbonic acid, and is an effect (Kemmerich) of ferments of a foreign nature. In all probability this is a case of the origin of fat by the oxidation and splitting up of albuminous bodies (Hoppe). Finally, the amount of casein increases at the expense of the albumin without the addition of air or a ferment (Kemmerich).

During the period of lactation the amount of milk secreted at both breasts in twenty-four hours amounts to about 1350 grammes.

Separation.

The withdrawal of the milk out of the flask-shaped reservoirs of the milk-ducts is brought about, as a rule, by the sucking of the young animal for whose nourishment the secretion serves, *i.e.* by atmospheric pressure. The smooth muscular fibres, which surround the whole gland, probably assist. A portion of the muscles further subserves the purpose of the erection of the nipple, which has as yet been insufficiently investigated, and which ceases to occur after section of the cerebro-spinal nerves of the mammary gland (Eckard).

6. Secretions for the Sense Organs.

We have here to do almost entirely with the secretion of mucous glands, for which the same description will serve as was given in the section on Alimentary Secretions. In addition there are the cerumen of the ear (p. 119), and the secretion of the Meibomian glands (p. 121), which have been already mentioned. It only remains, therefore, to describe the secretion of tears.

Tears.

Tears are secreted by the racemose lachrymal gland, which is exactly similar in construction to the glands secreting mucus. The secretion itself may also be regarded as a very watery mucus (or saliva): it consists of a large proportion of transuded material, together with small amounts of mucin and albumin.   It is clear, colourless, alkaline, and of a saline taste.

Tears contain 99 per cent. of water, 0·1 per cent. of albumin, 0·8 per cent. of salts, 0·1 per cent. of epithelium (Frerichs).

Tears are continually secreted in small quantities (Chapter X.).   Their secretion is, however, considerably increased by certain kinds of psychical stimuli, or, in a reflex manner, on irritation of the nasal mucous membrane, the conjunctiva, or the retina. The impulse to secretion occasioned by irritation of the nasal mucous membrane only extends to the gland of the side stimulated (Herzenstein). The nerves, irritation of which increases secretion, and which therefore contain the secretory fibres, are the lachrymal branch of the trigeminal, the subcutaneous malar branch of the same nerve, and the cervical sympathetic. Reflex stimulation proceeding from the nose may occur after section of the lachrymal nerve (Herzenstein).

The tears reach the conjunctival sac by several excretory ducts. Concerning their further application and destination, consult Chapter X.

The specific secretions of the generative organs, in which morphological structures are the essential constituents, are treated of in the fourth Section of this book.

CHAPTER III.

RECEPTION OF MATERIAL INTO THE BLOOD.
ABSORPTION.

The Materials Absorbed.

THE substances which are taken up (absorbed) into the blood are :—

1. The oxidizing body, oxygen, absorbed in the process of respiration (Chapter IV.).

2. The food or material destined for the repair of the tissues, or for the replacement of those portions of the body which are separated and cast out unchanged. Certain preparatory processes have to be passed through before absorption is possible ; such processes are denominated digestion.

3. The products of the chemical changes of substances which, having been absorbed by the blood and carried to the various organs of the body, have there undergone oxidation. The bodies thus formed are either gaseous (carbonic acid being the only instance) or liquid. They are, moreover, either the ultimate products of oxidation which the blood takes up simply in order to convey them to situations specially appropriated to their excretion (carbonic acid, urea, &c.) ; or they are compounds which are not made use of at any particular spot, but are further decomposed either in the blood itself, or after their resecretion in some other situation. To this class belong most of the so-called ' specific constituents ' of the various secretions, whether parenchymatous juices, the fluids of cavities, or free secretions, the only difference being that in the first case the constituents are re-absorbed by the blood in the place where they were secreted, while in the case of the free secretions they undergo reabsorption in other situations after they have

traversed for a longer or shorter distance the channels or canals of the body.

4. Finally, a considerable amount of the materials separated from the blood in the course of secretion are reabsorbed unchanged, either elsewhere, or, if the physical conditions have in the meantime become altered, in the very place of their secretion ; such substances are water, salts, albumin, called collectively 'transuded materials.'

Further explanation of the substances included in the third class will be given on p. 138. The fourth class includes the unaltered constituents of the parenchymatous juices and fluids of cavities, as well as of pathological transudations (œdematous fluids, serous effusions). Their re-absorption into the same vessels and under the same conditions as obtained during secretion would, of course, be impossible. The conditions therefore must be changed (*e.g.* the filtration-pressure of the blood, which is continually altering, must diminish), or absorption must take place by another way (*e.g.* through the lymphatic system). The unaltered constituents of true secretions are reabsorbed elsewhere than at the place of secretion.

Methods of Absorption.

Absorption of material into the blood takes place in part directly into the blood-capillaries, and in part indirectly through the lymphatic vessels which constitute an appendage to the blood-vascular system. The capillaries of blood-vessels and lymph-vessels lie everywhere together. The lymphatic vessels proceeding from the alimentary apparatus, and especially from the intestine, are called lacteals.

The lymphatics and the lacteals form a simple, branched, vascular tree (comparable with that of the veins), which opens into the jugular veins at their bases by two inconsiderable trunks, viz., the thoracic duct and the right lymphatic duct. The latter receives lymph only from the vessels of the right upper portion of the body and the right half of the thorax, while the thoracic duct collects the lymph from all the remaining vessels, including the lacteals. But few accurate observations have as yet been made concerning the origin of the lymphatic vessels in the various organs. Some regard the closed network of capillaries (which are somewhat wider than blood capillaries) as the commencement, while others suppose this network to originate in the fine, wall-less, spaces of the tissues. In many compound tissues, especially in glands, the lymphatic vessels commence in fissure-like spaces between the blood-vessels and the other components of the tissue, *e.g.* the glandular canals or ducts (Ludwig, Tomsa, Zawarykin, Mac-Gillavry). In the spinal cord these spaces surround the blood-vessels as perivascular spaces (His). These lymph-spaces appear to be lined by epi-

thelium. The so-called serous sacs (pleura, peritoneum, &c.), and the sub-cutaneous lymph-sacs of the frog, constitute similar but much larger lymphatic spaces. They are lined by epithelium and filled with lymph (p. 92); and they communicate, by means of small openings ('stomata') occurring between the epithelium cells, with the lymphatic capillaries of the neighbouring tissue, *e.g.* with those of the centrum tendineum of the diaphragm (von Recklinghausen, Ludwig and Dybkowsky, Schweigger-Seidel and Dogiel, Oedmannson), and especially with those of tendons and fasciæ (Genersich).

The origin of the lymphatic vessels within the elementary tissues themselves must most probably be sought (Virchow) in the retiform canalicular systems, which, according to Virchow's theory, are formed by the anastomosing cells of those tissues (connective tissue proper, bone, &c.); or which, according to von Recklinghausen, are systems of tubes bearing at their nodal points the protoplasmic masses characteristic of the tissues in which they occur. It is possible that this system of canaliculi stands, on the other hand, in direct communication with blood-capillaries, in which many observers suppose inter-epithelial openings—stomata—to occur.

The same uncertainty is felt regarding the origin of the lacteals in the villi of the small intestine. The villi are small, closely-packed processes of the mucous membrane, of various shapes, but mostly conical, which give the inner surface of the small intestine the appearance of velvet. They are covered with the columnar epithelium of the intestinal mucous membrane, and possess smooth, longitudinal, muscular fibres, which produce in them a shortening and a spiral twisting on contraction (Brücke). Each contains, besides a net-work of capillary blood-vessels, the disputed commencement of the lacteal, which leaves the villus as one, or sometimes several, small vessels. These lacteals originate in some way in the epithelial cells covering the villi; for all bodies which reach the chyle-vessels from the intestine must first pass through them, as may be demonstrated in the case of fat-globules. Some suppose a direct union of epithelium cells, through the canalicular system of the connective tissue of the villi, with the lacteal vascular system, which communicates, by means of processes, with the united bases of the epithelium cells (Heidenhain, Eimer, von Thanhoffer). Others suppose a capillary system of lacteal vessels to exist within the villi, which is, however, closed, and can only communicate by diffusion with the cells of the epithelium (E. H. Weber). A third set of observers deny the presence of such capillaries (Funke, Kölliker), and even of the central lacteal (Brücke, Basch); and think that the substances absorbed from the intestine pass through wall-less spaces, through the meshes of the tissue composing the villi, or through fissures between the blood-vessels and the surrounding tissue (Basch). The same views, therefore, are held respecting the origin of lacteals as of lymphatics. The nature of the epithelium cells themselves is as much disputed as that of the origin of the lacteals. The fact that they are capable of taking up bodies from the intestine (fat-globules, pigment-granules, blood-corpuscles, &c.) has led to the supposition of openings. Each cell presents to the interior of the intestine a thickened striated end where, if at all, the disputed openings must exist.

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According to some this end consists simply of a stopper of mucus, the cells themselves being, therefore, open. Others regard the striated appearance as indication of the existence of fine perforations (Kölliker, Welcker), or of a closely-packed bundle of rods filling up the orifice, and reminding one of cilia (Funke, Brettauer and Steinach, Heidenhain, Lipsky), the interspaces of which would therefore correspond to the perforations of the preceding observers. Others, again, think that the ends are quite imperforate. A theory propounded by Letzerich differs from all those just mentioned in supposing the particles which have succeeded in reaching the lacteal vessels to have traversed certain goblet-shaped structures, situated between the epithelium cells, which anastomose below with the canalicular network. These goblet-cells are thought by some (Eimer, F. E. Schultze) to be essentially secretory in function. Others regard them as simply the results of the method of treatment (Dönitz, Lipsky, Erdmann, Sachs), or as metamorphosed epithelial cells (Armstein, Oeffinger, Heidenhain). The glandular organs connected with the lymphatic and lacteal systems of vessels will be described below.

Forces concerned in Absorption.

The physical forces which are able to bring about an absorption of fluids into the blood (excluding those concerned in the absorption of gases, which are treated of in Chapter IV.), are, in the cases where it occurs through closed capillary walls, filtration and diffusion. The former in all probability only acts exceptionally, as it appears to be quite abnormal for the pressure without the vessels to exceed that of the blood within them.

Absorption into the lymphatic and lacteal vessels, the nature of the commencement of which is, as has been said, yet doubtful, is probably assisted by additional forces; such as, for instance, capillary attraction, in the case of open tubes. Filtration also may play a more prominent part here, as the pressure in the lymphatic vessels is considerably less than in the blood-vessels (Noll). It is impossible to say what substances are absorbed directly into the blood, and what through the lymphatics. As, however, from the uncertainty shrouding the lymphatic and lacteal systems, we are allowed to theorise more freely with respect to the forces concerned in absorption, we may suppose that substances which do not diffuse at all, or only with great difficulty—in short, whose absorption by the blood-vessels is to all appearance difficult or impossible—are taken up by the lymphatics or the lacteals. To this class of bodies belong especially solutions of albumin and fats, as well as finely

divided solids (colouring matters). Water and true solutions (including peptones) are most probably taken up by both systems of vessels. The absorption of fats, also, does not appear to be confined entirely to the lymphatics, as is indicated by the greater amount of fat in the blood of the portal vein, which receives the venous blood from the intestines, as compared with what is found in the blood from other vessels (Chapter V.).

An immigration of cellular structures into the blood-vessels, corresponding to their emigration described on p. 81, has been recently observed (von Recklinghausen, Saviotti). If those cells should contain in their interior finely divided colouring matters, fats, &c., a species of direct absorption of undissolved substances would thus be accomplished.

In frogs whose hearts have been destroyed, fluids are still capable of absorption from the lymph-sacs, so long as brain and spinal cord are intact (Goltz). It seems as if absorption ceases in vessels whose tonus is completely destroyed, as soon as they have become filled; while those, the nerves of which are active, are able again and again to expel their contents, thus permitting absorption to recommence (Bernstein, Heubel).

Seats of Absorption.

One of the chief seats of absorption, which must now be considered separately, is the alimentary canal. The constituents of food are here partially taken up, after having undergone the changes necessary to prepare them for absorption, viz. digestion. At the same time an absorption takes place of the various alimentary secretions (mucus, saliva, gastric-juice, pancreatic-juice, bile, intestinal juice), probably in a partially altered condition, after they have performed their several functions: certain of their constituents (mucin, the specific constituents of bile) are however not absorbed, being passed out of the system in the fæces. The changes brought about in digestion, which will be more fully described below, consist in the conversion of materials, such as starch, albuminous bodies and gelatin, which are unfitted for absorption, into modifications which are easily diffusible, viz. sugar, solutions of peptones and of gelatin. A small portion also of the fat is converted into easily absorbable soap (p. 106), the rest being emulsionized. Altogether, therefore, in the alimentary canal there are the following substances which undergo absorption :

1. Water derived partly from the food and partly from the alimentary secretions. 2. Soluble salts, also in part derived

from the insoluble salts, or the free acids and bases, taken in with the food. 3. Different kinds of sugar, all of which are derived from the food, grape sugar being, in addition, present as the result of the conversion of starch. 4. Other soluble constituents of food or of the alimentary secretions (pepsin, etc.). 5. Soaps formed from the fatty materials of the food. 6. Soluble albumin and the alkali-albuminate formed during digestion. 7. Peptones derived from the soluble and insoluble albuminous constituents of food. 8. Solutions of gelatin derived from the gelatin and gelatigenous elements of food. 9. Emulsionized fat (fat in fine globules) from food. Of the above substances those included in the first eight classes would appear, on account of their diffusibility, to be absorbed both by blood-vessels and by lacteals. All the true solutions (those mentioned in classes 1–4) are probably chiefly absorbed by the blood-vessels, or, perhaps, equally by them and the lacteals; but the remaining substances are for the most part taken up by the latter. The absorption of fat, on the contrary, seems to be confined almost entirely to the lacteals.

The way in which fat reaches the lacteals is, according to the various views stated on p. 129, either through complete canals (openings in the epithelium of the villi, communicating, through the canalicular system of the connective tissue, with the central lacteal of the villus, Heidenhain); or along paths which the fat-globules find out for themselves.

In either case, the action of bile in facilitating the filtration of fat (p. 106) is most important. The forces, however, which bring about absorption are still doubtful; the most probable is that of filtration under the somewhat high pressure in the intestines, since the pressure in the lymphatic system is slight. Contraction of the muscles of the villi can only force the contents of the lacteals within the villi towards the larger vessels of the system, rendering no assistance whatever in the absorption of fat from the interior of the intestine. This contraction is said to be facilitated by the action of the bile (Schiff).

The absorption of fat by the lacteals is well shown by the white, milky contents of those vessels after the ingestion of fatty foods; and the favourable action of the bile in promoting it is proved by the diminution in the contents which occurs if the admixture of bile be prevented by closure of the ductus choledochus, or the formation of a biliary fistula.

A second seat of absorption is the external skin, which, although only exceptionally active, is so often spoken of in connection with absorption that mention will be made of it here. All substances absorbed at the skin must first pass through the epidermis. The permeability of this structure appears to be usually very slight; but it may be much increased by various means (warm baths, etc.). The power of absorption possessed by the skin is proved by well-established facts.

The absorption of parenchymatous juices is still a matter of which little is known. It would appear that, apart from the absorption of those products of oxidation which are really soluble, the unaltered, albuminous constituents of transudation-fluids are constantly, or under certain circumstances, taken up by the lymphatics, and the more quickly according to the rapidity with which transudation takes place, *i.e.* according as the pressure of the parenchymatous fluids in the tissues is greater. Lymph, at least, will flow from an open lymphatic vessel the more quickly according as transudation is increased either by dilatation of the arteries proceeding to the part (by section or paralysis of vaso-motor nerves), or by prevention of the escape of blood (by ligature of the veins, or compression of them by muscular contractions), (Ludwig, Schwanda). The lymphatics, therefore, may possibly have to be regarded as regulators of turgescence. The condition in which there is increased pressure of the parenchymatous fluids, and which is remedied by increased activity of the absorbents, is called *œdema*. We may say that a system of drainage is continually in operation in the tissues, in which fluids are poured out of the blood-vessels by transudation, percolate the surrounding cellular tissues, and finally flow away through the lymphatics. The commencements of the lymphatic vessels are, as a rule, removed as far as possible from the blood-vessels (von Recklinghausen). Absorption from parenchymatous tissue appears to be promoted by pressure such as that exerted by the contraction of neighbouring muscles (Genersich). Increase of arterial blood-pressure has no influence upon the formation of lymph (Paschutin).

Destination of the absorbed Materials.

The substances absorbed directly into the blood at once form part of the plasma, from which they are in part excreted, and in part secreted, in other organs.

It remains now to follow in their course to the blood the substances which are indirectly absorbed through the lacteals and lymphatics. During this course they do not remain unaltered. Their composition is materially modified after passage through certain organs, the lymphatic glands, which form part of the lymphatic and lacteal systems of vessels. They are converted into a fluid which resembles in many respects the blood into which it is about to be poured, and is, as it were, a preparatory stage of it. As these organs are not only found in the course of the larger lymphatic vessels (as ordinary lymphatic glands), but also at the very commencement of the lymphatic and lacteal systems (as the so-called follicles), it is not possible to procure the original fluid as it exists immediately after absorption. The names chyle and lymph are, therefore, used to denote the modified contents of the absorbent vessels, which have already traversed glands.

The follicles, which have recently come to be regarded as the simplest form of lymphatic gland, are found in great numbers at the commencement of the lacteal and lymphatic vessels. Those connected with the former set of vessels, the lacteals, are buried in the intestinal mucous membrane, either singly ('solitary glands,' in the whole intestine), or in numbers together ('Peyer's patches,' 'agminated glands,' in the lower part of the small intestine). Those connected with the lymphatics are discovered in various parts of the body, especially in the mucous membranes of the mouth, the pharynx (the tonsils, also, are simply collections of follicles), the stomach, and the conjunctiva, in the lungs (described for a long time as small lymphatic glands), the spleen (Malpighian bodies), and probably also in many other situations. For a description of the intimate structure of the follicles and lymphatic glands, the student must refer to the Manuals of Histology; but the following account seems to embody all that is essential in their formation:—Follicles contain one, and lymphatic glands many, cavities (alveoli, lymphatic spaces), bounded by a network of connective tissue, and traversed by a delicate reticulum of fibres and blood-capillaries; the meshes of this reticulum are closely packed with colourless, round, nucleated cells (lymph-cells). These cell-filled spaces appear to be nothing but an extended canalicular system of connective tissue, the ground-substance of which has shrunk into the fine network or reticulum of fibres. Into these

spaces open either the usual connective-tissue canaliculi, or, in the case of lymphatic glands proper, the branches of the lymph-vessels proceeding to them which surround the alveoli as fissures (lymph-sinuses) lined with epithelium. From the alveoli pass out the efferent lymphatic vessels. All fluids, therefore, traversing the lymphatic system of vessels must pass through these alveoli and find their way between the cells, in which case they are brought into a relationship with the blood in the capillaries which is favourable to osmosis.

Lymph is a colourless or whitish-yellow fluid which is separable under the microscope into a colourless plasma and certain nucleated contractile cells (lymph-corpuscles), fat-globules and free nuclei suspended in it. Lymph-corpuscles resemble very closely the cells contained in the alveoli˙ of the follicles and lymphatic glands, and, undoubtedly, for the most part, originate from them. Before passing through the larger lymphatic-glands, lymph contains very few of these corpuscles, which it obtained from the follicles, or from the connective-tissue canaliculi (p. 129) and probably also from the blood-vessels (p. 81). They completely resemble the white corpuscles of the blood. When removed from the living body, lymph coagulates like blood, only more slowly, a lymph-clot being formed while a lymph-serum is squeezed out by its contraction. It therefore contains fibrin-formers, and generates the ferment (p. 52), but not to the same extent as blood,—hence the addition of blood hastens coagulation. The remaining constitutents of lymph are exactly similar to those of blood, with the exception of the colouring matter, which is wanting, viz. water, salts, alkali-albuminate, protagon, fats, sugar, urea, extractives and gases (almost entirely composed of carbonic acid, Hammarsten). Chyle is difficult to obtain pure, as it is constantly mingled with lymph in the receptaculum chyli and thoracic duct. It is distinguished from the latter fluid by the greater quantity of fat it contains during digestion, which gives to the vessels containing it a milk-white appearance. The fat forms single or united globules, larger than those of lymph. It is, moreover, taken up by the contractile lymph-corpuscles.

The motion of the lymphatic fluids towards the blood takes place under a slight pressure (Noll) and very slowly, chiefly on account of the considerable resistance which the lymphatic glands must offer. The forces which sustain this motion can only be guessed at: they are probably:—1. Those forces which

bring about absorption of the contents into the initial branches of the system, and which, as was explained previously, are yet unknown : their effect must be to cause a gradual progression of the lymph or chyle.   2. The contraction of the various muscles surrounding the lymph-vessels, which, on account of the numerous valves existing in those vessels, forces the lymph towards the larger trunks, just as is the case in veins (p. 67). 3. The aspiration of the thorax (p. 66); for the openings of the principal trunks, and the greater part of the thoracic duct also, lie within the thoracic cavity.

In amphibia and certain birds (Ratitæ), the movement of the lymph is assisted by the rhythmical pulsation of lymph-hearts, of which four exist in the frog, two in other amphibia, and one in the ostrich. The central nervous organ connected with this rhythmical motion is said by some to be in the spinal cord, and by others in the hearts themselves. In guinea-pigs a rhythmical contraction has recently been observed (A. Heller) in the lymphatics of the mesentery. As this proceeds along those portions of the vessel between the valves with a regular progression towards the larger trunks, it must be regarded as a species of cardiac mechanism.

When the lymph has reached the blood vessels it mingles with the blood.   What further use is made of it, and how it is transformed, will be described in Chap. V.

Preparation of Food for Absorption.

Digestion.

In the alimentary canal, which stretches from the mouth to the anus, the food, which has been taken into the body in a solid or liquid form, is in part directly absorbed through the walls, thus coming to mix with the juices of the tissues.   The greater portion, however, has first to undergo a certain mechanical and chemical preparation.   Those constituents of the food which are incapable of absorption either directly or after having passed through the various stages of digestion—the indigestible constituents—pass out of the body *per anum*, in company with certain portions of the alimentary secretions, as fæces.

I. THE CHEMISTRY OF DIGESTION.

The secretion and properties of the alimentary juices have been described in the preceding chapter.

Water, the inorganic constituents of food, and, for the most part, the soluble organic constituents also, undergo no essential chemical alteration in the alimentary canal. If they are already dissolved, or are soluble in the secretions of the canal, they are absorbed unchanged whenever they reach the situations where absorption is possible ; while, if they are in the form of free acids and bases, they are firstly combined. Certain substances upon which the alimentary juices are unable to act, and which are insoluble, also remain unchanged : to this class belong especially cellulose, and horny and elastic tissues. Such, moreover, is the fate of that portion of the soluble substances which escapes solution owing to the superabundance of the quantity ingested or to the closeness of texture of the body. All such materials disappear from the body *per anum*, together with certain portions of the digestive juices. The air which happens to be swallowed with the food yields up its oxygen in the alimentary canal and receives in its place carbonic acid (Chap. IV.) ; hence, in the large intestine, it is chiefly nitrogen and carbonic acid which are found. The essential chemical changes of digestion chiefly concern certain insoluble, or dissolved but hardly diffusible, organic bodies, which rank among the most important elements of food ; viz. carbohydrates (especially starch); albumins (albumen, fibrin, the substance of muscle, casein, etc.), both soluble and insoluble modifications; gelatin ; and fats. These substances must be converted into some form which admits of absorption.

Herbivores appear to possess some arrangement for the digestion of cellulose, probably for its conversion into sugar. We are led to the supposition of a digestion of cellulose in such cases by a consideration of the large amount of it contained in vegetable foods, and the almost complete absence of it from other nutrient substances which seem nearly incapable of supporting life in those animals. In man, also, it has recently been observed that the cellulose taken into the body along with food cannot be completely recovered from the fæces (Henneberg and Stohmann, Weiske). It is not known which secretion acts upon it. The cuticular substances, also, which

are said to contribute to the building up of hippuric acid, must undergo digestion in the alimentary canal of herbivores, while to carnivores they are indigestible.

In the cavity of the mouth food is saturated with the alkaline fluid resulting from the mixture of saliva from the parotid, submaxillary and sublingual glands with mucus from the mouth. This saturation affords opportunity (1) for the solution of soluble, but as yet undissolved, portions of food (*e.g.* salts, sugar), and (2) for the conversion of the starch contained in the food into dextrin and grape-sugar. This conversion begins while the food is yet in the mouth and is continued in the stomach if the quantity of acid there is not sufficient to retard it (p. 94).

In the stomach the following operations take place : (1) An intimate mingling of all portions of the food with one another and with the secretion of the gastric glands, viz. mucus and gastric juice. As the latter has an acid reaction the previously alkaline mixture becomes for the most part neutralized or acidified. Many constituents of it, which were before undissolved, undergo solution in the stomach, especially such salts as are only soluble in the presence of an acid, as, for instance, the carbonates and phosphates of the alkaline earths. (2.) The conversion of starch-mucilage into sugar by means of the swallowed saliva, which continues as long as the acid reaction is not too strong. (3.) The modification of albuminous bodies, which is the chief change effected in the stomach. Fibrin, and the substance of muscle, reach the stomach almost always in an insoluble form ; albumin is sometimes soluble and sometimes insoluble (*e.g.* boiled white of egg), as also is casein which is dissolved in milk, and undissolved in cheese. Dissolved casein is, however, precipitated by the gastric juice immediately on its entrance into the stomach. As a rule, therefore, both soluble and insoluble modifications of albumin are submitted to the action of the gastric juice. Under the influence of the acid of the gastric juice undissolved albumins swell up in the stomach, and thereupon become dissolved by means of the pepsin and converted for the most part into peptones (p. 31). Soluble and insoluble albuminous substances are equally well digested (Fick). Gelatin, also, and gelatigenous tissues (connective tissue, the stroma of bone) are converted in the stomach

into an ungelatinizable solution. It is not certain whether the time during which food remains in the stomach is sufficient for the completion of the above-mentioned changes ; but, after a liberal allowance of food has been taken, quantities of un-altered starch and undissolved albuminous substances pass into the intestine. The contents of the stomach after passing into the intestine form a pulp, for the most part acid, which is called *chyme.*

Natural digestion in the stomach has been observed, in man, through gastric fistulæ which have been the result of accident (Beaumont, Bidder and Schmidt), and, in the lower animals, through fistulæ which have been made artificially. Observations have also been made upon food which had been enclosed in network bags and swallowed, and, after having remained in the stomach for a certain time, withdrawn by means of an attached string. From experiments with natural or artificial gastric juice at the temperature of the body (artificial digestion), many confirmations of the processes which go on in the stomach have been obtained.

* In the intestine the acid chyme comes into contact with secretions which are entirely alkaline, viz. with bile and pan-creatic juice in the duodenum, and with intestinal juice in the whole intestine. This must bring about, in the first place, a change in the reaction, which occurs earlier in those portions of the contents of the intestine touching the walls than in those which are nearer the centre. Towards the middle of the small intestine the change is complete, and the reaction is, therefore, at that point alkaline. Although the properties of each of the alimentary secretions are separately known (as was seen in the preceding chapter), little has been discovered con-cerning their action when mixed together in their normal con-dition. It has been shown that intestinal digestion, so far as it concerns the chemical changes of the contents of the intes-tines, and not their absorption, produces the same effect on the yet unaltered starch and undissolved albuminous and gelatinous portions of the chyme as digestion in the preceding parts of the alimentary canal. The starch, therefore, is converted into sugar, and the albuminous substances and gelatin into soluble peptones. It is also known that the fats, which have hitherto remained unaltered, are here prepared for absorption. The formation of sugar out of starch must be ascribed to the pan-creatic juice, as the saliva from the mouth can no longer with

certainty be shown to be present. Solution of the albuminous bodies is effected most probably by the pancreatic, and intestinal juices, as the activity of the gastric juice which reaches the intestine is destroyed by the bile (p. 99). Peptones are in part further decomposed in the intestine (p. 107), for which purpose their precipitation by the bile (p. 105) appears to be of importance, as they would be otherwise too quickly absorbed. As the result of this further decomposition leucine and tyrosine are formed, and, since they cannot be discovered in the fæces, are probably soon afterwards absorbed. Other products of the decomposition help to form the fæces. Finally, fats are converted into a very fine emulsion by the pancreatic juice (and probably also by bile and intestinal juice), in which form they are fitted for absorption. A portion of the fats is decomposed by the pancreatic juice into fatty acids and glycerin, which are also soluble and capable of absorption. The last-named effect of pancreatic juice does not appear to occur until the contents of the intestine have assumed an alkaline reaction, *i.e.* until the lower half of the small intestine has been reached. The fatty acids resulting from the decomposition combine with alkalies to form soaps, which, in their turn, aid in the emulsionization of the remaining portion of the fats (Brücke).

Besides the above decompositions, which are of the highest importance for absorption, others occur which are of no moment apparently in the promotion of that process. Thus, cane-sugar, when taken into the body, is converted into grape-sugar owing (according to Paschutin) to a peculiar ferment of the intestinal juice. Grape-sugar, both when taken as food and when formed in the course of digestion, as well as milk-sugar, are in part changed into lactic acid prior to absorption, this change taking place while they are yet in the stomach. Alcoholic and butyric acid fermentations also occur, but probably only under abnormal conditions. The gases which are yielded in these fermentations are principally carbonic acid and hydrogen, but sometimes also light carburetted hydrogen (marsh gas). The intestinal gases, therefore, consist chiefly of carbonic acid, nitrogen and hydrogen (Chapter IV.). Salts of the organic acids, moreover, are said to become entirely or in part converted into carbonates while yet in the intestine (Magawly). The fatty acids resulting from the decomposition of fats are further split up, yielding gases and volatile products, which, together with the ill-odoured bodies formed during pancreatic digestion (p. 107), endow the otherwise almost odourless contents of the small intestine with their characteristic fæcal smell. The conjugate bile-acids undergo a hydrolytic decomposition in the small intestine, probably under the influence of the

pancreatic juice; glycocine or taurine, as ¦the case may be, and cholic acid, are the products, and the latter passes into the fæces partly in the form of its anhydrides, choloidic acid and dyslysin.

In consequence of the chemical changes which have just been described, and of the succeeding absorption of fats and all those constituents which were soluble or had been rendered soluble, the contents of the small intestine become considerably altered in composition as they pass along the alimentary canal. Starch and the insoluble albuminous bodies which were still present at the commencement of the intestine gradually disappear, and instead of them we meet with sugar, lactic acid, peptones, leucine and tyrosine. The larger globules and masses of fat, also, which at first were mingled with the other substances, are no longer found, having formed an emulsion. The colour is yellow or yellowish brown, owing to the admixture of biliary colouring matters. Finally, all the dissolved diffusible matters and fats disappear entirely from the mass, and the amount of water present becomes continually less and less, until at the extremity of the small intestine nothing is found but the constituents of the fæces already possessing the characteristic odour on account of the above-mentioned decompositions and fermentations.

In the large intestine the digestive processes (*i.e.* the preparation for absorption) become less and less apparent. No new secretions are added, except the intestinal juice, which is formed here also, and absorption is restricted to water, the result being a concentration of the contents. The latter, consisting of fæces and gases, have already been described.

The fæces often exhibit an acid reaction, which is due to the presence of free fatty acids. The amount of the fæces as compared with the amount of the food taken depends, of course, upon the quantity of indigestible materials contained in the latter.

The chemical processes of digestion have throughout the character of hydrolytic decompositions (Hermann), as a comparison of the results of digestion with the bodies submitted to that process will show. These decompositions not only appear to be favourable to absorption, inasmuch as their products are for the most part more diffusible than the original substances; but they seem to have far more important func-

tions in 'assimilation' or the construction of the constituent parts of the body out of the nutritive materials. (Concerning this matter consult Chapters V. and VI.)

II. THE MECHANISM OF THE DIGESTIVE APPARATUS.

The mechanical operations of the digestive apparatus comprehend : 1. The introduction of the food into the mouth, its propulsion along the alimentary canal, and the evacuation of the fæces. 2. The mechanical preparation for absorption, viz. the breaking-down of solid foods and their intimate mixture with the various fluids destined to effect their chemical preparation (mastication, insalivation, etc.). These processes go on side by side.

The introduction of food is accomplished, in the case of fluid substances, by a combination of the acts of pouring into the mouth and sucking up by means of it (drinking); and in the case of solid substances by placing small pieces behind the lips and teeth, or by cutting or biting off small pieces from a larger piece by means of the incisors.

Mastication, or the breaking down of the firmer portions, begins immediately after the introduction of a piece of solid food into the mouth. It commences with a division of the food, by means of the knife-like incisor teeth, into small pieces, which are thereafter ground down between the irregular surfaces of the molar teeth at the back of the mouth. The operation of cutting is effected by an up and down movement of the lower jaw, *i.e.* by a rotation of it about a horizontal axis passing through its two articulations. The upward movement is produced by the masseter, temporal and internal pterygoid muscles, and the downward movement by the weight of the lower jaw, and by the action of the digastric, mylo-hyoid and genio-hyoid muscles, the hyoid bone being kept firm by the omo-hyoid, sterno-hyoid, thyro-hyoid, and sterno-thyroid muscles. The grinding is produced by a motion of the articular heads of the inferior maxillary bone in their sockets in such a manner that the lower jaw is displaced with respect to the upper jaw in an anterior, posterior and lateral direction. This is accomplished in particular by the two pterygoid muscles. The morsels

of food are continually pushed between the teeth by the muscles of the cheeks and lips, especially by the buccinator on the outside, and by the tongue within. The latter, moreover, has the power of crushing down softer portions of food by pressing and rubbing them against the hard palate. During digestion the food is intimately mixed with the fluids of the mouth (saliva and mucus) and forms a plastic pulp.

The nerves which control these actions are, for the proper masticatory muscles, the inferior maxillary branch of the trigeminal (particularly its superior division) and for the tongue and a portion of the abductors of the lower jaw, the hypoglossal. The centre for the co-ordinated masticatory movements is situated in the medulla oblongata (Schröder van der Kolk). In many animals the action of the saliva, and, in part also, the breaking down of the food, are continued in certain apparatus connected with the stomach; as, for example, in the first three stomachs of ruminants (rumen, reticulum, and psalterium), from the first two of which the imperfectly masticated food passes into the mouth before being transferred to the third; in the crop and gizzard of many birds; in the masticatory stomach of beetles; in the toothed stomach of crabs; &c.

The propulsion of solids and fluids along the alimentary canal is effected by the contraction of the circular and longitudinal muscles of its walls, which takes place in such a manner that the diminution or closure of the lumen of the canal drives the contents before it in a direction from the mouth to the anus. These propulsive contractions are called peristaltic movements; or, when occurring in the first portion of the alimentary canal from the mouth to the œsophagus—in which case they are effected by voluntary muscles—swallowing. In the act of swallowing two stages are distinguished:—1. The bolus of food situated on the anterior part of the tongue, which forms a groove with concavity upward, is pushed along towards the anterior arch of the fauces by the progressive application of the tongue to the hard palate from before backwards. 2. *a.* The anterior pillars of the fauces close-to by the contraction of the palato-glossal muscles, and, at the same time, the root of the tongue approaches the velum palati. *b.* The posterior pillars of the fauces, also, with the aid of the uvula, close-to and block up the passage between them, and the whole velum is then drawn upwards and backwards and apposed to the posterior wall of the pharynx by means of the pharyngo-palati and the levator and circumflexus palati. *c.* The hyoid bone and the larynx

are approximated by the action of the thyro-hyoidei, and drawn strongly forwards and upwards by the genio-hyoidei, mylo-hyoidei, and the anterior bellies of the digastric muscles, the lower jaw, which is kept apposed to the upper by the muscles of mastication, being the fixed point. By this means the root of the tongue is bent backwards and pressed, together with the epiglottis, upon the opening of the larynx. By the actions given under *a*, a return of the food into the cavity of the mouth is prevented, by those under *b*, its passage into the pharyngeal cavity and the nose, and by those under *c*, its passage into the larynx. The morsel, therefore, propelled by the progressive contraction of the constrictors of the pharynx and the stylo- and salpingo-pharyngei, has no way left for it except into the œsophagus. While in the neighbourhood of the tonsils, which are rich in mucous glands, it becomes slimed over with mucus, and its further movement is thereby facilitated.

Even in the absence of the epiglottis, the closure of the opening into the larynx can be effected, but less securely, by the root of the tongue. The recess or pouch between the root of the tongue and the epiglottis is so completely closed during the act of swallowing, that no portion of the fluids swallowed is able to enter it, as may be proved by the absence from it of any colouration after coloured liquids have been drunk.

The tongue as a whole is drawn downwards and somewhat forwards by the genio-glossal, downwards and backwards by the hyo-glossal, and upwards and backwards by the palato-glossal and stylo-glossal, muscles. All these muscles, as well as the lingualis, traverse the substance of the tongue in a vertical, transverse, or longitudinal direction. By their contraction in various combinations, the tongue is able to assume the most diverse forms; thus, flattening is produced by contraction of the vertical fibres; extension and thickening by contraction of the vertical and transverse fibres; shortening by contraction of the longitudinal fibres; channelling of the upper surface by contraction of the transverse and the inner set of the vertical fibres; arching of the upper surface by contraction of the inferior transverse fibres; lateral flexion of the tip by contraction of the longitudinal fibres of one side; &c.

In the œsophagus the morsel of food, well covered and rendered slimy by mucus, is driven downwards into the stomach, partly by its own weight, but chiefly by the peristaltic movements of the walls, which are occasioned in the lower two-thirds by the contraction of unstriped muscular fibres only.

In the stomach the larger portions of food remain for a longer time. The movements which take place there are not as

yet well understood. This much may however be said : on the
one hand the various parts of the contents of the viscus must be
kneaded together and intermixed, and the internal portions
thus made to come into contact with its walls; and, on the
other, the food must be driven along the stomach and finally
through the pylorus. The latter result is effected by the peri-
stalsis, which occurs in every part of the alimentary canal.
How these two varieties of movement are produced, and how
they change one into the other, is almost unknown. In all
probability the gastric walls are usually contracted closely upon
their contents. The muscular fibres, which are present in
greater numbers around the cardia and pylorus, ordinarily
keep those orifices closed. The constant closure of the former
has, however, been recently disputed (Giannuzzi). The closure
of the pylorus is firmest at the commencement of digestion,
relaxing gradually as it proceeds, so as to allow the passage into
the intestine, first of fluids, then of chyme-pulp, and finally even
of solid material. The stomach, in course of becoming filled,
rotates about a horizontal axis passing through the cardiac and
pyloric openings, in such a manner that the great curvature,
which usually hangs down, is turned forwards. This is not pro-
duced by any muscular action, but is a purely mechanical effect.
Gases, which are swallowed with the food or are evolved in the
stomach, pass out for the most part through the cardiac opening,
which lies highest. The movements of the stomach are said to
cease during sleep (Busch).

Peristaltic movement is most marked in the small intestine.
It is associated with a varying disposition of the coils of the
whole intestine, except the closely confined duodenum, and is
constantly directed towards the anus. It gradually propels the
somewhat fluid contents, as well as the enclosed gases, until they
pass into the cæcum. Movement in an opposite direction is
hindered by the valvular folds of the intestinal mucous mem-
brane, and a return into the small intestine from the cæcum
(the special object of which is unknown) is prevented by the
ileo-cæcal valve, a fold of the intestinal wall.

In the large intestine peristalsis takes place very slowly, the
contents being therefore able to remain in the sinus-like dilata-
tions of the colon for a longer time. After continuing there
until, by the loss of their fluid constituents, they have assumed

the characters of fæces, the contents reach the sigmoid flexure, and finally the rectum.

Evacuation of the fæces from the rectum takes place, as a rule, at intervals of twenty-four hours. Besides the peristaltic movement of the intestinal tube, the pressure of the abdominal muscles plays an important part in the operation, not indeed by acting directly upon the rectum, which lies secure in the bony pelvis, but probably by forcing the fæces from the upper parts of the canal. (The mechanism of this pressure of the abdominal muscles will be discussed in Chap. IV.) The sphincters of the rectum are, as a rule, closed. Their contraction, and, when that is removed, their elasticity, is overcome by the pressure of the fæces driven downwards by the forces above mentioned. The levator ani prevents the protrusion of the rectum, and, by shortening it, facilitates the liberation of the contained mass of fæces.

Liberation of the Movements of the Digestive Apparatus.

The propulsive movements of the alimentary canal are occasioned only by the stimulus of its contents. They appear therefore to be induced in a reflex manner. The movements of swallowing, for example, only occur—but then always—when a foreign body is placed behind the soft palate. They take place, therefore, whenever the posterior surface of the velum palati, the epiglottis, &c. are touched. Hence the simple act of swallowing can only be voluntarily performed, in the absence of other stimuli, by bringing some saliva behind the soft palate; and this explains why it is only possible 'to swallow nothing' a few times in succession, viz. only as long as there is any saliva in the mouth.

The nervous centres for the striated muscles concerned in the movements of the upper part of the alimentary canal lie in the medulla oblongata, and in man, in the olivary bodies (Schröder v. d. Kolk). The nerves thence proceeding which regulate the act of swallowing are : the facialis for the lips ; the nerves of mastication (see above) for the jaws ; the hypoglossal nerve for the tongue ; and the plexus pharyngeus (formed from the glosso-pharyngeal, vagus-accessorius and sympathetic nerves) for the pharynx. The tensor palati and the mylo-

hyoideus are provided for, in addition, by the trigeminal
nerve. The sensory fibres, irritation of which induces swallow-
ing, lie in the palatal branch of the trigeminal nerve (Schröder v.
d. Kolk). The peristaltic movements of the remaining portions
of the canal probably have their central organs in the ganglia
of the walls, some of which are known to exist, while the
rest must be assumed (Remak, Meissner, Manz, Billroth,
Auerbach, Krause). The presence of ganglia explains the
movements of excised portions of intestine. Direct stimulation
brings about local contraction which sometimes, but by no
means constantly, continues as peristalsis. All parts of the intes-
tine are, however, provided with extrinsic nerves, derived espe-
cially from the vagus (plexus œsophageus, rami gastrici) and from
the sympathetic (splanchnics, cœliac, mesenteric and hypogastric
plexuses). These are undoubtedly in part concerned in the
movements. All that has as yet been clearly demonstrated,
however, is (1) that irritation of the vagus is able to produce
contractions of the œsophagus and stomach ; (2) that section
of the vagi prejudices to an important extent the passage of
food out of the stomach ; and (3) that irritation of the splanch-
nics inhibits the peristaltic movements of the small intestine
(Pflüger) ; the latter may therefore be included among the
class of ' inhibitory ' nerves (Chap. X). In the evacuation of
fæces the nerves of the expiratory muscles, as well as of the
levatores ani and other muscles, are also concerned.

The movements of swallowing can also be induced by stimulation of the
larynx ; as also on irritation of the superior laryngeal nerve (Waller and
Prevost).

In the frog the movements of the throat and stomach become very
active after section of the vagi, or destruction of the cerebro-spinal organs ;
it has therefore been supposed (Goltz) that the vagi exert an inhibitory
influence upon them.

The movements of the intestine cease in warm-blooded animals if the
temperature sink below 19° C. : they become more active as the tempera-
ture increases ; interruption of the flow of blood to the organ stops them
(Horwath). As in the ureter, the transmission of peristalsis in the intestines
is considered to be due to direct muscular conduction (Engelmann and van
Brakel). The circumstance of transmission taking place in one direction only
is, however, opposed to this.

The movements of the intestine are stopped by saturating the blood with
oxygen, and increased during suffocation. They are, for this reason, probably
very active immediately after death. It would seem that the stimulus leading

to the liberation of the intestinal movements, analogous to that causing the movements of respiration, is dependent upon the venous state of the blood in the intestinal vessels (S. Mayer and von Basch).

The splanchnics are, at the same time, the vaso-motor nerves of the intestine; irritation of them, therefore, occasions a diminution in the amount of blood flowing to the viscera. This may possibly explain the inhibition of peristalsis, which it also produces. For the rest, if the intestinal vessels are emptied, *e.g.* by compressing the aorta, increased movement results, which ceases on again injecting the vessels with some fluid (O. Nasse). After death, or, more exactly, at a time when the vessels are paralysed, and the capillaries contain venous blood (Mayer and von Basch), irritation of the splanchnics and irritation of the vagi both produce intestinal movements. The effects of irritation of vagi are contested, or ascribed to the contraction of the stomach, which drives the contents into the intestine (van Braam, Houckgeest).

The occurrence of anti-peristaltic movements of the intestine, although frequently maintained, is not yet proved. Vomiting, *i.e.* the evacuation of the contents of the stomach through the mouth, consists, not in an active contraction of the stomach, but in the compression of it by the contraction of the diaphragm and the abdominal muscles (Magendie). This is shown by the fact that vomiting is still possible after the substitution of a bladder in place of the stomach (Magendie). It is, however, necessary for the success of this experiment to remove the cardia and the lowest portion of the œsophagus along with the stomach (Fantini, Schiff). Vomiting, moreover, can no longer take place after poisoning by curare, which paralyses voluntary motion, while it leaves intact the nerves going to the stomach (Giannuzzi). Active movements of the stomach, consisting especially of an active opening of the cardiac orifice (Schiff), may be observed in an exposed stomach during the then unsuccessful attempts at vomiting. This opening of the cardiac orifice is necessary before vomiting can occur. The central nervous organ for the act of vomiting is closely allied to the respiratory centre. Emetics prevent the occurrence of apnœa (Chap. IV.); and strong artificial respiration prevents vomiting. It would seem, therefore, as if emetics had the power of strongly irritating the respiratory centre (Grimm). This irritation also results, from an action of centripetal nerves, on injection of the emetic into the blood (Kleimann and Simonowitsch).

Purgatives act, according to some (Moreau), by increasing the secretion of the fluids of the intestine, and according to others (Thiry, Radziejewski) by quickening the peristaltic movements. Saline purgatives, the activity of which depends upon their endosmotic equivalent (Buchheim), and which when injected into the blood-vessels produce costiveness (Aubert), act chiefly by causing the retention of water in the intestine (Buchheim).

CHAPTER IV.

GASEOUS INTERCHANGES (INCOME AND EXPENDITURE) OF THE BLOOD.

Respiration.

BY the term Respiration we designate those chemical processes of the animal body which are concerned in the distribution of gaseous substances, *i.e.*, essentially those concerned in supplying oxygen to the constituents of the body, and in separating the gaseous product of oxidation—carbonic acid.

• This process, like all others connected with the interchange of matter between the animal body and the outer world, is carried on through the agency of the blood. This fluid comes into contact, on the one hand, with the medium in which the animal lives (atmospheric air or water), abstracting from it oxygen and giving up to it carbonic acid (external respiration); on the other hand, with the animal tissues, to which it furnishes oxygen and from which it abstracts carbonic acid (internal respiration). External respiration, which is briefly denominated *Respiration*, takes place wherever the blood comes into sufficiently close contact with the respiratory medium, but chiefly in the organs specially devoted to the gaseous interchanges, and which are denominated *The Organs of Respiration.*

Atmospheric air is a mixture composed of about one-fifth (0·208) by volume of oxygen, and four-fifths (0·792) by volume of nitrogen, together with a very small and fluctuating quantity (from 0·0003 to 0·0005 by volume) of carbonic acid, and a similarly fluctuating quantity of aqueous vapour, the maximum amount of which depends upon the temperature. This mixture, at the level of the sea, is under a pressure of about 760 millimetres of mercury.

The water, which serves as the respiratory medium for many organisms, contains in solution, besides some nitrogen and carbonic acid, oxygen, which at a temperature of 15° C. and 760 millimetres pressure, amounts, at the most, to one-twelfth (0·084) part of its volume. Corresponding to this small amount of oxygen, animals living in water require proportionally little of that element.

I. CHEMISTRY OF RESPIRATION.

External Respiration.

Respiration, properly so called, which consists in the interchange which takes place between the gases of the blood and those of atmospheric air, has its seat wherever the blood-capillaries are in intimate contact with the latter medium. This occurs especially at the external surfaces of the 'Organs of Respiration,' which will be discussed below, and, in addition, at the skin and in the alimentary canal which always contains air, though in both these cases the process goes on with feeble intensity.

In some animals, however, *e.g.* in frogs, cutaneous respiration (perspiration) is of such importance that, after the lungs have been removed, it suffices by itself to supply the small quantity of oxygen which the animal requires.

Intestinal respiration, in consequence of the slight supply of gas, is insignificant in man ; still all the oxygen contained in the alimentary canal is consumed and replaced by carbonic acid, so that in the large intestine carbonic acid and nitrogen are the principal gases.

In many animals (*e.g.* in an air-swallowing fish, cobitis fossilis), intestinal respiration appears to be important.

Cutaneous respiration was formerly supposed to be of great importance, even in the case of warm-blooded animals, as its suspension, brought about by varnishing the shaven skin, causes a rapid fall of temperature and death (Bernard). According to recent researches (Rosenthal and Laschkewitsch), there always occurs in such cases a dilatation of vessels over the varnished area, which, when it extends to the whole body, occasions such a loss of heat as to prove fatal. This paralysis of vessels, according to others, likewise occurs in internal organs, the morbid processes in which (as in the kidneys and spinal cord) play a part in inducing the symptoms (Feinberg, Socoloff).

Further, there are some who attribute the injurious consequences of varnishing the skin to the retention in the body of a deleterious excrementitious substance ('perspirabile retentum'); this appears to consist of a volatile nitrogenous compound. From portions of the skin which have been left uncovered by the varnish, an elimination of a volatile alkali (ammonia ?) may be discovered by means of hæmatoxylon paper. Subsequently an inflammatory œdema occurs in the portions of skin which have been long kept covered with varnish, and in the serum, crystals of phosphate of mag-

nesium and ammonium can be found (Edenhuizen); possibly the retained substance is urea, which is decomposed and generates ammonia (Lang).

External respiration consists in a passage of oxygen from the air into the blood, and of carbonic acid, aqueous vapour and heat from the blood into the air. Respired air, therefore, leaves the body poorer in oxygen, but hotter and richer in carbonic acid and water, being almost saturated with the vapour of the latter. Corresponding to the changes in the air, the blood which leaves the lungs, in the pulmonary veins, is richer in oxygen, cooler (?), and poorer in carbonic acid and water, than the blood of the pulmonary artery. It is, consequently, of a more florid (arterial) colour. Only a small portion however of the loss of heat and of water which takes place is suffered by the blood in the lungs, as all parts of the respiratory passages give up heat and aqueous vapour to the inspired air.

Traces of ammonia are also excreted in the process of respiration (Thiry), but apparently in pulmonary respiration only (Schenk), so that the ammoniacal compounds which are observed when the skin has been varnished would appear to be abnormal products.

In spite of the loss of heat which the blood must undergo in the lungs, the blood of the left side of the heart, according to recent observations (Colin, Jacobson, and Bernhardt), is not cooler, but warmer than that of the right; possibly because a production of heat takes place in the lungs, owing to its combining with oxygen (Colin). This statement is denied by others (Heidenhain and Körner). (Consult Chap. VII.)

The cause of external respiration is, in great part, if not entirely, the difference between the tension of the gases in the blood and in the external atmosphere, respiration consisting in the equalization of those tensions.

The tension of the oxygen in venous blood, *i.e.* in blood which is to be subjected to the respiratory process, is smaller than the tension of the oxygen in the atmosphere, while the tension of the carbonic acid in the former is, on the other hand, greater than that in the latter. This is true not only of pure atmospheric air, but also of the air which is contained in the pulmonary alveoli, and which is much poorer in oxygen and richer in carbonic acid. In virtue of the very low tension of the oxygen of its blood, an animal placed in a confined space can consume almost the whole of the oxygen which it contains, whilst the evolution of carbonic is very soon stopped by an equalization of the tensions taking place (Wilh. Müller).

To determine the tensions of the gases of any specimen of blood, it must be agitated with a limited volume of the gases; the tensions of the components of the latter after agitation (ascertained by determining the composition and the total pressure), are a direct measure of the tension of the gases of the blood (Ludwig).

Strictly, such an experiment merely teaches the tension of the gases in the blood after agitation. Hence the result is more correct, the smaller the difference in the gaseous tension of the blood before and after agitation, *i.e.* when the quantity of blood experimented upon is relatively large, the volume of the gases used small, and when the tension of those gases represents closely the previous gaseous tension of the blood under investigation. In order to obtain the most correct results, the blood is simultaneously but separately agitated with two volumes of gas, of which the one possesses a somewhat higher, and the other a somewhat lower tension than the gases of the blood subjected to investigation; the true gas-tension of the blood is then found by taking the mean of the tensions of the two samples of gas which have been in contact with it ('Aerotonometer' is the name given to an apparatus devised for this purpose by Pflüger and Strassburg).

The tension of the oxygen of the blood is, in consequence of the affinity of hæmoglobin for it, very low; but it becomes higher when the blood is heated (Worm Müller). In the arterial blood of the dog it amounts on an average to 22 millimetres of mercury (*i.e.* it corresponds to the tension of the oxygen of an atmosphere which contains 2·9 per cent. of oxygen); in venous blood it amounts to 29·6^{mm} (3·9 per cent.). The tension of the carbonic acid is, in arterial blood, on an average 21^{mm} (2·8 per cent.), in venous blood 41^{mm} (5·4 per cent.) (Strassburg).

The tension of the oxygen in the external atmosphere amounts on an average to 158^{mm} (20·8 per cent.), the tension of carbonic acid to 0·38^{mm} (0·05 per cent.).

The tension of the carbonic acid in the air contained in the pulmonary alveoli is so high that it may appear doubtful whether it does not exceed the tension of the carbonic acid in ordinary venous blood. Were such the case, one would have to suppose that certain influences were in operation in the lungs, capable of driving off the carbonic acid, *i.e.* of increasing the tension of the carbonic acid of the blood entering the lungs. Such influences have, indeed, been sought for partly in the absorption of oxygen, and partly in the action exerted by the lung tissue itself. To determine this point, the tension of the carbonic acid of the blood contained in the lung capillaries is directly ascertained by shaking the blood with a known quantity of the

air removed from the lungs, and analysing the air before and after the process (Becher). As, however, when the breath is held, the tension of the gases of the blood is very much altered, and as the air which is removed from the lungs has not equally taken part in the equalisation of tension, it is a better plan to remove, for this purpose, by means of a lung-catheter, only the air from a single portion of the lung of an animal (Pflüger and Wolffberg).

From such experiments it results that the tension of the carbonic acid of the blood of the pulmonary capillaries of the dog is about equal to that of the venous blood of the heart (Wolffberg), so that external respiration is to be looked upon as consisting essentially of a simple equalisation of the tensions between venous blood and the air contained in the lungs. The rapidity of gaseous diffusion in the lungs is such that even when the respiration is free and quiet, the expired air of the dog possesses a carbonic acid tension which is nearly equal to that of venous blood (on an average 2·8 per cent CO_2 and 16·6 per cent. of O, Wolffberg).

Nevertheless, it is possible that the simultaneous absorption of oxygen in the lungs helps to drive off the carbonic acid, though to what extent is unknown. The tension of the carbonic acid of the blood is found to be greater when the blood is agitated with a gas containing oxygen than with one containing no oxygen, or than when the blood is placed in an empty receiver (Ludwig and Holmgren : Wolffberg).

Oxygen, therefore, increases the tension of the carbonic acid of the blood, by exerting a chemical action which serves to expel carbonic acid. Further, it is found (Ludwig and Schöffer, Sczelkow, Preyer) that arterial blood is not only poorer than venous blood in carbonic acid which may be pumped out of it, but also in carbonic acid existing in more stable salt-like combinations. Lastly, the carbonic acid tension of serum is much lower than that of the blood as a whole, and is increased by the addition of blood, though not by merely passing oxygen through it. From these facts we should conclude that the blood corpuscles which contain oxygen exert a chemical action, by which carbonic acid, especially that existing in the serum, is liberated from stable compounds, in a form capable of being pumped out of the blood.

According to J. J. Müller, when blood is made to flow through the blood-vessels of a lung inflated with nitrogen, it

gives up more carbonic acid than when it is placed in a simple chamber containing nitrogen. These researches, which ascribe some share to the lung-tissue in causing the expulsion of carbonic acid, have recently been disputed (Pflüger and Wolffberg).

The action of the blood corpuscles referred to in the previous paragraph, and which apparently can only depend upon the formation of an acid, may be imagined to take place in various manners: 1. Oxy-hæmoglobin, which has an acid reaction (Preyer), might itself possess the power of expelling CO_2 (Preyer); in support of this hypothesis, amongst other facts, may be mentioned, that passing oxygen through blood furthers the crystallisation of hæmoglobin, just as does diminishing the alkaline reaction of the blood by the addition of acids (Kühne).

2. Oxygen might bring about a decomposition of hæmoglobin, leading to the formation of an acid (in certain decompositions of hæmoglobin, volatile fatty acids are generated, Hoppe-Seyler). When the gases of the blood are pumped out under such circumstances that evaporation goes on to a great extent, the strongly combined carbonic acid of blood, even, for instance, that derived from carbonates added to the fluid, is expelled (Pflüger); it is conceivable that in this case acids are generated by the decomposition of hæmoglobin.

3. The acid might originate in other constituents of the blood-corpuscles. *e.g.* in lecithin.

4. If carbonic acid contained in the blood corpuscles were in a state of combination, say with hæmoglobin, it is possible that oxygen might expel it directly. Even in lung-tissue, whose influence in aiding the elimination of carbonic acid was suspected, an acid occurs, to which the power of expelling CO_2 was formerly ascribed, viz. taurine. (Cloetta; formerly this body was described under the name of pulmonic acid by Verdeil). As certain albuminous compounds (globulin) liberate carbonic acid from carbonates *in vacuo*, an attempt has been made to make use of this fact in the explanation of the respiratory process (Hoppe-Seyler and Sertoli); this explanation does not, however, agree with the fact that oxygen has a more powerful action in expelling the carbonic acid of the blood than a vacuum.

Seeing that respiration proper consists in an equalisation of the tensions of the gases existing in the blood and in the air of the pulmonary alveoli, it follows that the blood in the lungs is the richer in oxygen and the poorer in carbonic acid, the closer the air of the alveoli approaches in composition to atmospheric air. And this will depend upon the energy of the respiratory process, that is to say, upon the frequency and depth of the respiratory movements which influence in an important manner the gaseous constituents of the blood, and so indirectly exert an influence upon the gaseous interchanges

of the whole organism. It is only by comparing the air inspired and expired during long periods of time that we can form a correct estimate of the gaseous exchanges of the body.

Respiration of the Tissues.

The question as to the seat of the respiration of the tissues is the same as that of the seat of the oxidation-processes which go on in the animal body. The ancient view (Lavoisier) that carbonic acid was generated in the lung itself is disposed of by the fact that the venous blood which goes to that organ contains large quantities of carbonic acid.

The increase in the quantity of carbonic acid has to be traced back to the capillaries. And it must be either within these vessels, or in the tissues outside of them, that the consumption of oxygen and the formation of carbonic acid proceed. The first of these two views, viz. that which places the seat of oxidation within the capillaries, is improbable, because oxidation-processes are so closely linked to the functions of organs that they must occur within them. The question would be most easily solved if we could compare the tension of the gases contained in the tissues with the tension of the gases of the blood. In general, such a comparison is impossible. The tension of carbonic acid in cavities and in fluids of the body which are surrounded on all sides by healthy tissues (as, *e.g.*, in intestinal loops and in the contents of the gall and urinary bladder) is decidedly greater even than in venous blood, pointing to the fact that the tissues give up carbonic acid to the blood; but to the place where carbonic acid originates, oxygen too must wander (Pflüger and Strassburg).

Another method of determining indirectly the tension of the gases of the tissues, would be to investigate the tension of the gases of the lymph (Ludwig and Hammarsten). In this fluid the tension of the carbonic acid is lower than in venous blood, though higher than in arterial blood. We must not from this fact conclude that carbonic acid does not originate in the tissues, seeing that the lymph experimented upon has had the opportunity, both in the connective tissue and in the lymphatic vessels, of modifying the tension of its gases by close contact with arterial blood.

One, though by itself a very insufficient, ground, for placing the seat of oxidation-processes within the vessels, appeared to be the occurrence of easily oxidisable substances (reducing substances) within the blood, especially in the blood of asphyxiated animals (A. Schmidt). The source of the latter

substances, which are contained in the blood corpuscles and not in the plasma (Afonassieff), may lie in the blood itself; lymph contains none of these substances (Hammarsten). The oxygen tension of many tissues appears to be almost equal to nothing, so that they must eagerly absorb oxygen. Muscle, for instance, contains no oxygen capable of being pumped out of it (Hermann, Chap. VIII.).

The energy of internal respiration naturally varies in the case of different organs, and in each organ it varies with the time, according to the energy of the processes of oxidation which go on within it. A comparison of the gases and of the colour of the blood of the arteries and veins of an organ supplies a measure of this energy. The blood of the renal veins is almost arterial in colour, whilst that of muscles is very dark. In the latter it appears to be more florid during activity, probably because the greater gaseous exchanges are more than compensated for by the increased flow of blood through them (Chap. VIII.).

The nature of the oxidation-processes which go on in the tissues strictly do not belong to the study of respiration; yet they must be briefly alluded to in this place.

In muscles, which are the organs in which they have been chiefly studied, oxidation does not go on directly, for the processes of absorption of oxygen and formation of carbonic acid do not occur simultaneously. (On this subject further information will be found in Chap. VIII.). On that account the theories which connect the oxidation-processes of the body with a process of ozonizing of the oxygen, or with a formation of peroxide of hydrogen, are improbable.

Magnitude of the Gaseous Exchanges.

The magnitude of the gaseous exchanges of the body, leaving aside the variations occasioned by the movements of respiration, is chiefly dependent upon the amount of oxygen which the organism requires (for this requirement see Part II.). The more the blood is charged with carbonic acid produced in the processes of oxidation of the body, the larger the quantity of carbonic acid which is given up. Amongst the circumstances which increase either the individual or combined processes of oxidation, the following are specially to be emphasized: muscular work; a low temperature of the medium surrounding the body (which increases the production of heat in the body, so as to maintain the normal temperature, Chap. VII.); the process of digestion (which is connected with the increase of many secre-

tions); great energy of all the vital processes (as in persons of the male sex, of strong constitution, in the prime of life, &c., and in cold-blooded animals during a rise in temperature). All these circumstances increase the evolution of carbonic acid, for in all oxidation-processes of the body carbon is oxidized. Those processes increase the excretion of carbonic acid the most which are connected with the combustion of highly carbonaceous substances, as, for instance, the consumption of a diet rich in carbo-hydrates, which, in part, appear to be directly burned. The consumption of oxygen need not necessarily proceed exactly simultaneously with the evolution of carbonic acid, even when all the carbonic acid which is formed is immediately excreted : for, on the one hand, a formation of carbonic acid is conceivable without oxygen being needed (the carbonic acid being one of the products of a process of decomposition), and, on the other hand, oxygen may, in some way, be stored up, and not be used at once. (Further information in reference to this process may be obtained in Chap. VIII.)

From what has been stated it follows that the numbers given below, which express the average magnitude of the gaseous exchanges, possess comparatively little value :

An adult man requires in 24 hours about 746 grammes (520 litres) of oxygen, and expires about 867 grammes (443 litres) of carbonic acid (Vierordt).

If all the oxygen were employed in the oxidation of carbon, and all the carbonic acid formed were expired, the volume of the latter would, over considerable periods of time, be equal to the volume of oxygen, seeing that a molecule of CO_2 and a molecule of oxygen (O_2) occupy the same volume. As, however, other oxidation-processes occur (leading to the formation of H_2O, &c.), and as a portion of the carbonic acid formed is excreted in the urine, &c., it follows that the carbonic acid formed must occupy less space than the oxygen consumed, so that when an animal breathes in a confined space, a rarefaction of the air takes place. (The latter circumstance is explained also by the fact that the consumption of oxygen proceeds until the supply is exhausted, whilst the separation of carbonic acid soon diminishes and ultimately ceases.

By the influence of work the consumption of oxygen *per hour* may increase from 31 grammes (see above) to about five times this amount (156 grammes. Hirn).

In man the interchange of gases through the skin, as compared with that at the lungs, is almost imperceptible. The carbonic acid excreted in 24 hours varies between 2·3 and 6·3 grammes, being on an average 3·87 grammes; its amount increases with the temperature (Aubert).

The daily experience that exhaled air is warmer and moister than the at-

mosphere, and the simple experiment of breathing through a tube which dips into lime- or baryta-water, which becomes turbid in consequence, suffice to show qualitatively the differences between inspired and expired air.

In quantitative comparison, as the composition of the air inspired is known, it suffices to investigate the air expired, which for this purpose is collected in a mercurial gasometer (Allen and Pepys). The air which is breathed is freed from carbonic acid and water by passing it through caustic potash and sulphuric acid.

In order to determine the total gas-exchanges which go on during long periods of time, the expired air may be allowed to pass through an apparatus in which the carbonic acid and water formed are absorbed, so that they may both be weighed. For this purpose appliances for aspirating are required, *e.g* a vacuum (Andral and Gavarret), a vessel containing water, which is allowed to run out (Scharling), or an air-pump (Pettenkofer). If the research has to be carried out on a large scale (as in Pettenkofer's apparatus, the air-space of which can conveniently supply a man for some time), it suffices to allow only a measured fraction of the in-going and out-going air to pass through the absorbing fluids, provided that the total volumes of the gases are continually measured (by means of gas-meters).

According to another method, respiration is carried on in a completely confined space, which is in communication only with an oxygen reservoir; the carbonic acid formed is continually being absorbed by a connected apparatus containing solution of caustic potash; in consequence of the diminution of pressure which results from the absorption, oxygen is continually being sucked from the reservoir. At the end of the experiment the amount of carbonic acid absorbed by the caustic potash is determined, as well as the nitrogen which was originally present in the chamber; the oxygen which has been used, is found by ascertaining the diminution which the store of this gas originally present in the chamber and the connected reservoir has undergone (Regnault and Reiset). Similar, though simpler, apparatuses have lately been constructed (Ludwig and Kowalewski, Ludwig and Sanders-Ezn).

When the gaseous exchanges dependent upon the whole external respiration have to be determined, the respiratory space surrounding the whole body must be investigated. If only the respiration of the skin is to be investigated, the mouth and nose are made to communicate with the exterior by means of a tube; finally, if only the pulmonary respiration be the object of research, the respiratory chamber is in communication by an airtight mask with the mouth and nose.

II. THE MECHANISM OF RESPIRATION.

In the lowest organisms, the bodies of which are but small, the mere bathing of the body in the medium to be breathed (water) is sufficient to keep up the interchange of gases by diffusion; more highly developed animals of larger size require a larger surface for the proper interchange between the juices of the body on the one hand and the medium on the other. In animals

in which the blood-vascular system is either in a rudimentary state or altogether wanting, the medium must be introduced into and distributed over all parts of the body in order to be everywhere brought into contact with the juices; but where the blood-vascular system is fully developed, the mass of the blood can be passed into an organ of large surface, where it can meet the medium to be breathed, and where, thus, on large surfaces the blood can enter with it into the process of diffusion.

The arrangement in the first class consists of a system of branched tubes, as in the *water-vascular system* of echinodermata and scolecida, and the *tracheal system* of arthropoda: while in the latter class we have an *eversion* of the body surface if water is breathed, as in the *gills* of mollusca, fishes, and the larvæ of batrachia; or an *involution* if air is breathed, as in the *lungs* of amphibia, birds, mammals, and man. As a separate respiratory medium for the fœtus of mammals and of man, we have the oxygenated maternal blood, which meets the blood of the fœtus in the placenta (fœtalis and uterina), where through the walls of the capillaries the gaseous exchange takes place (Chap. XII.).

The human respiratory organs,[1] the lungs, represent two elastic bags, containing a branched system of tubes with terminal vesicles (alveoli), and the surface in each alveolus being further extended by the presence of prominent ridges in its walls. The cavity of each lung communicates by means of the trachea, larynx, pharynx, and the nasal or oral cavity, with the external air.

The lungs left to themselves contain no air : they are *atalectic*, like the lungs of the fœtus before it has ' breathed,' *i.e.* the walls of its tubes and of its alveoli lie in apposition by virtue of their elasticity. In the human body, however, the lungs are so fitted into an unyielding reservoir (the thorax) that no air can pass between their external surface and the internal surface of this reservoir (more accurately, between the pleural surface of the lungs and the lining of the thorax). The pressure of the atmospheric air entering the lungs must necessarily therefore expand them against their own elasticity to more than their normal volume : they closely apply themselves to the thoracic walls, and are therefore during life always found filled with air. Should, however, through any opening, air pass into the space between the lungs and the thoracic walls, then the lungs by virtue of their elasticity collapse to their natural (atalectic) volume (Pneumothorax).

[1] The cutaneous and intestinal respiration (p. 150), not possessing a separate mechanism, are not considered here ; their importance in man is but small.

Not only the lungs, but the heart and vessels also, contribute towards the filling up of the thoracic cavity. The pressure of the air acts upon the inner surface of all these organs; it acts directly (through the trachea) on the lungs; it acts indirectly on the heart, for the whole body, and therefore all the vessels situated outside the thorax, and communicating with the interior of the heart, are under atmospheric pressure. The same pressure then tending to enlarge all the hollow organs within the thorax, these organs will expand according to their degree of expansibility, and hence the most expansible organs, the lungs, will contribute most towards the filling up of the thorax (they will be dilated the most beyond their original volume), the thick-walled ventricles the least, while the thin-walled auricles and the venous trunks (p. 5) will be perceptibly dilated. The atmospheric pressure acting equally upon the external surface of the thoracic walls, their more yielding parts will likewise contribute towards the filling up, or rather the diminution of the thorax: hence the diaphragm and the intercostal spaces will arch in towards the thorax.

The following model illustrates these relations. A bottle provided with a stopcock, o, contains two elastic bags, represented in fig. 1 in their natural
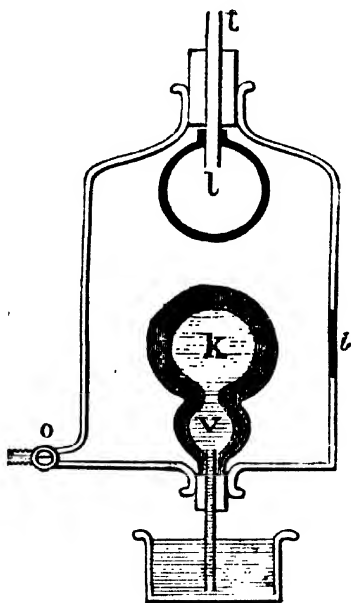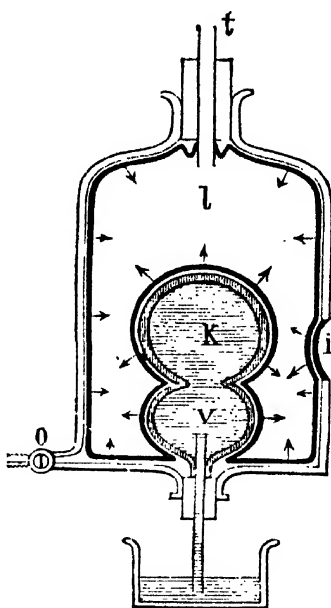

FIG. 1.   FIG. 2.

configuration; the one, hourglass-shaped, with a thin-walled and thick-walled division, v and k, is filled with a fluid and communicates with an open vessel containing water; this double bag represents the heart (v = auricle, k = ventricle), the other bag, *l*, filled with air and communicating through *t* (= trachea) with the atmosphere, represents the lung. The membrane *i* represents the soft parts of an intercostal space. Fig. 2 shows the apparatus after the air has been exhausted, through o, from the bottle. Both bags, on

the inner walls of which the atmospheric pressure acts (indirectly on v κ), are seen expanded, filling up completely the interior of the bottle; *l* is most expanded, v much less, and κ the least; *i* is also seen to be somewhat vaulted in. If now through o air is again allowed to enter, we get again the same condition of things as in fig. 1, which corresponds to the condition of pneumothorax.

Each of the two bags in fig. 2 tends to contract at the expense of the other, *i.e.* to extend the other. The figure represents the state of equilibrium. Hence in the usual representation of the relations in the thorax, lungs expanded above their normal volume are made to exercise a pull ('negative pressure') on the heart and the soft parts of the thoracic walls (represented by arrows in fig. 2), but we have also to consider that the heart, &c. acts in the same way on the lungs.

We are able to measure manometrically the elastic force with which the lung, when expanded to the size it has in the passive thorax, tends to contract (or in other words, its negative pressure when the thorax is at rest), by fixing a manometer air-tight into the divided trachea of a dead body and then opening the thorax; this elastic force is about 6 mm. of mercury (Donders). The elastic force of the expanded lung may be further assisted by the non-striped muscles surrounding the bronchial tubes, for by their contraction the bronchial tubes would be narrowed, and therefore the negative pressure in the thorax increased, whereby a greater expansion of the other organs would be effected. We know, however, nothing definite either about the time and mode of this contraction or about the innervation of the muscles. Irritation of the pneumogastric diminishes slightly the volume of the lung, when the latter is cut out and ligatured (Schiff).

The Respiratory Movements.

The air contained in the alveoli of the lungs enters into relations with the gases of the blood circulating in the capillaries surrounding the alveoli. These relations, as already stated, consist, on the part of the air contained in the alveoli, in a loss of oxygen and a gain of carbonic acid, whereby this air is soon rendered unfit for any further gaseous exchanges. Owing to the diffusion of gases, however, an exchange between the gases contained in the alveoli and the separate layers of the super-imposed air is possible, and this exchange will eventually reach the external air; but as it will only take place in layer after layer, it will be too slow to effect a thorough removal of the gases of the blood : it will be necessary therefore that the air in the alveoli be repeatedly and mechanically renewed, and this is effected by a regularly alternating expansion and con-traction of the *thorax* (inspiration and expiration), which the lungs of necessity must follow.

The expansion of the thorax, *Inspiration,* is always pro-
duced by muscular action. The regularly acting inspira-
tory muscles are: the *Diaphragm,* the *Scaleni* and *Intercostal*
muscles, particularly the *external* intercostals. In deep or (on
account of obstacles) laboured inspiration, other accessory in-
spiratory muscles are called into play, namely, the *Serrati
postici* and the *Levatores costarum* ; and, when there is great
difficulty of breathing, the *Sterno-cleido-mastoidei,* the
Pectorales and the *Serrati antici,* &c.

The expansion of the thorax is chiefly effected by the dia-
phragm, the muscular portion of which, in contracting, becomes
less convex, while its borders recede from the thoracic walls, to
which they are apposed when at rest. Nearly all the other muscles
act on the ribs : they generally run forward and downward, and,
their upper ends, which are attached to the vertebral column or
(Pectorales, Serrati antici) to fixed points of the upper extre-
mities, forming the fulcrum, they draw the ribs outwards and
upwards, whereby the thorax is expanded.

Each rib, having one of its two joints attached to the body of a vertebra,
and the other to the transverse process, is movable round an inclined axis;
each upward rotation round this axis will make the inclined plane pass-
ing through the curvature of the rib more horizontal, and will therefore
widen the diameter of the thorax. The rotation of the ribs round this axis

Fig. 3.
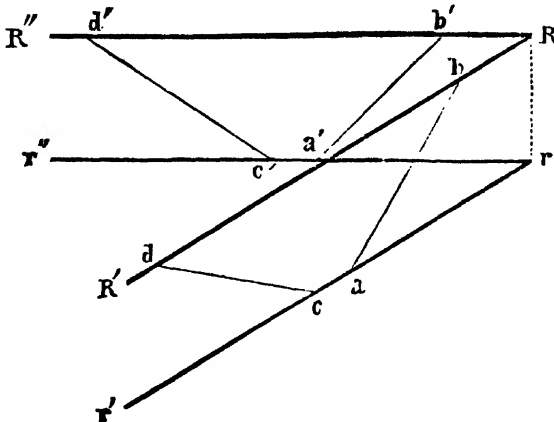
is, however, kept within narrow limits by the costal cartilages (though they
are elastic and somewhat yielding) which fasten the ribs to the sternum.
The action of the muscles which elevate the ribs is therefore easily under-
stood. How far the intercostals also are elevators of the ribs will be evident
from the following consideration (Hamburger).

In the accompanying figure RR′ and rr′ represent the posterior portions (passing forward and downward) of two consecutive ribs during rest; RR″ and rr″ the same during inspiration; ab represents a fibre of an intercostalis internus, cd a fibre of an intercostalis externus. It will be seen at a glance that the distance ab is less in the elevated position (a′b′), while cd is less in the lowered position.[1]

From this it follows inversely that the shortening of ab will elevate, the shortening of cd will lower, both ribs. Now, as the direction of the fibres is exactly the reverse in the *anterior* portion of the ribs (between the angle of the ribs and the sternum), the interni will here act as inspiratory, the externi as expiratory muscles; or, in other words, those externi attached to the bony parts of the ribs and those interni attached to the cartilaginous portions will act as inspiratory muscles; and as this corresponds nearly accurately to the chief seats of distribution of the two kinds of fibres, we may therefore consider the intercostals as inspiratory muscles. Experimentally, however, the action of the intercostals has not yet been definitely determined.

While the elevators of the ribs increase the transverse diameter of the thorax, the contraction of the diaphragm causes an increase of the longitudinal diameter. According as the movements of the ribs or of the diaphragm preponderate, do we distinguish between *costal respiration* and *abdominal respiration* (the latter name being derived from the fact that with the descent of the arch of the diaphragm, the contents of the abdomen are pushed downwards, in consequence of which there is protrusion of the abdominal walls). Costal respiration is chiefly observed in the female, abdominal respiration in the male, sex.

The diminution of the capacity of the thorax, *Expiration*, is brought about by the weight and the elasticity of the thoracic walls, by virtue of which they return to their position of equilibrium after the inspiratory forces which have forced them from this position have ceased to act. The weight of the ribs draws them down, the elasticity of the lungs draws the diaphragm upwards, and the thoracic walls inwards; the elasticity of the costal cartilages, which have undergone torsion, brings the ribs back again to their normal position. In forced and obstructed expiration, muscular force will also enter into play, the direction of the expiratory muscles being forwards and upwards. The principal expiratory muscles are: the abdominal muscles, the quadrati lumborum, the serrati postici inferiores, and the

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[1] Supposing the angle $rRb = x$, we have:

$$ab^2 = Rr^2 + (ra - Rb)^2 + 2Rr\ (ra - Rb)\cos x$$
$$cd^2 = Rr^2 + (Rd - rc)^2 - 2Rr\ (Rd - rc)\cos x\ ;$$

∴ ab will be the greater the smaller x is, while cd will be the greater the larger x is (the cosine increasing with the decreasing angle).

intercostales interni. The abdominal muscles compress by their contraction the contents of the abdomen—they therefore push the diaphragm up and draw the ribs down ; the quadrati lumborum and the serrati postici inferiores do the same, as do also the intercostals, as far as they run along the bony parts of the ribs. How the lowering of the ribs contracts the thorax will be evident from what has been said before.

The different apparatus which conduct the air to the lungs also take part in the respiratory movements : the *rima glottidis* dilates in inspiration, and in forced inspiration the *nostrils* are dilated by the levatores alæ nasi, thus facilitating the entrance of air to the lungs.

The lungs, as already stated, must of necessity follow every movement of the thoracic walls, and every inspiration will therefore cause an increase of capacity of the lungs, both in the transverse and vertical diameters. The parts of the lung close to the chest-wall will also participate in this movement, for the borders of the diaphragm recede with each contraction from the chest-wall. Every inspiration is naturally associated with a descent of the lung in the chest ; and this of itself would cause, even without any increase of the transverse diameter of the thorax, an increase in the transverse diameter of the lungs ; for the thorax is of a conical form, and by the descent every section of lung would be received into a deeper and therefore wider section of the thorax. The descent of the lung causes in its turn a lowering of the trachea and larynx, which is visible from without.

The expansion of the lungs with inspiration, which affects all their cavities, but particularly the more easily yielding alveoli, causes an increase in the volume of air they contain. This increase in calm breathing amounts to about 6 per cent. of the total volume ; deep inspiration causes, however, a much greater change. We have a measure for the limit of this possible change of air in the ' *vital capacity* ' of the lungs, by which we mean the difference between the volumes of air in the lungs when these are expanded and contracted to the fullest possible extent, or in other words the quantity of air which is expelled after the deepest possible inspiration by the deepest possible expiration (Hutchinson). This quantity is in nearly constant proportion to the size of the individual ; it varies, however, with

the occupation and the sex (being larger in men, Arnold). In grown-up persons its medium value is 3770 Cc.

To measure the vital capacity we use the 'spirometer' (Hutchinson), which consists in a gasometer, the receiver of which is kept in equilibrium by weights; into this gasometer we expire (through an india-rubber tube connected with it) after a deep inspiration; the volumes of air are measured by the proportional heights to which the cylindrical receiver is raised. Gasmeters may also be used for this purpose.

Other measurements to be considered are: *a.* The quantity of air contained in the lung after the strongest possible expiration ('residual air,' Hutchinson). This quantity may be determined by breathing hydrogen from a closed receiver till there is no longer any alteration in the composition of the gas, at which point the hydrogen will be uniformly mixed with the air in the lungs: by now expiring to the deepest possible extent, the amount of gas still contained in the lungs may be calculated from the composition of the expired gas mixture and the quantity of hydrogen which is missing (H. Davy, Gréhant). *b.* The quantity of air contained in the lungs at ordinary expiration (which is determined in the same way as above). The difference between these two quantities, or the quantity of air which after an ordinary expiration can still be expired, is called the 'reserve air,' or 'supplementary air:' in like manner the difference between the quantities of air at the ordinary and at the deepest possible inspiration is called the 'complementary air,' while the difference between the quantities of air at ordinary in- and expiration is called the 'respiratory air.' If we call the residual air a, the supplementary air b, the respiratory air c, and the complementary air d, then $a + b + c + d$ is the vital capacity.

As regards the chemical renewal of the gases in the lungs, it has been found (by inhaling hydrogen, Gréhant) that if a quantity, c, of a gas be inhaled between any two expirations, a certain quantity, $a. c$, of this gas remains in the lungs and is equally diffused (if $c = 500$ *c.c.*, $a. c = 330$). At ordinary inspiration, therefore, $\dfrac{a. c}{a + b + c}$ represents the volume of new air (in the chemical sense) which the unit-volume of the lung-cavity receives at each inspiration; this quantity (which, for instance, if $c = 500$ and $a + b + c = 2930$, is $\dfrac{330}{2930} = 0.113$) is called the 'coefficient of ventilation.' It has further been found (by a single inspiration of hydrogen, followed by ordinary respiration in air) that when the quantity of gas inspired is 500 *c.c.*, it is only after the sixth to the tenth respiration that it has all left the lung (Gréhant).

To determine the movements of the thorax the 'thoracometer' is used (Sibson), which measures the alterations in the horizontal median diameter of the chest. The anterior chest-wall pushes a small rod before it which by means of a spring moves an index: the axis of the index is fastened by a support to a board on which the body rests in a horizontal position. Similar apparatus (Ransome) measure at the same time the excursions in several diameters; they can also be so modified as to give graphic representations

(Riegel). The 'pneumograph' or 'atmograph' (Marey) is a belt, of which an elastic hollow cylinder, the lumen of which is extended by every inspiration, forms part. The pressure of the air in the cylinder is graphically registered. The variation in the diameter can be registered in the same manner as the variation in the circumference, by pressure transmitted through a column of air (Fick). In animals the movements of the diaphragm can be measured by means of a needle inserted into it, or by means of a lever pushed against the diaphragm from the side of the abdomen, which registers its movements graphically in curves on a paper passed before it ('phrenograph,' Rosenthal).

As the thorax expands with every inspiration, the hollow organs situated within it will also become expanded above the natural volume which they possess when at rest. Hence, amongst other results, 'the negative pressure' under which the heart and great vessels exist will increase, thus causing the aspiration exerted by them to increase also.

On the other hand, the negative pressure may be entirely removed, or even converted into a positive pressure by expiration, though ordinarily the latter merely restores the conditions existing before inspiration. This will occur when during active expiratory effort the air is prevented from escaping from the thorax by closure of the rima glottidis.

The effects of the aspiration of the thorax on the circulation in the lungs are according to some accelerating (Haller, Quincke, Pfeiffer), according to others retarding (Poiseuille, J. J. Müller). The pressure of the air in the respiratory passages (which during rest is equal to the atmospheric pressure) also undergoes slight variations, owing to the narrowness of the entrance (nostrils, rima glottidis), being about—1 mm. at inspiration, and 2–3 mm. at expiration. These variations can be determined, in animals by a manometer connected laterally with the trachea, and in man by a manometer which is attached to one nostril, the individual expiring through the other nostril, while he keeps his mouth closed.

The friction against the walls of the larynx and the system of tubes through which the current of air passes during each inspiration gives rise to *murmurs* audible by the ear applied to the chest-wall. In the unyielding parts (larynx, trachea, and larger bronchi) this murmur has a more whiffing, breezy character (= *h* or *ch*, 'bronchial murmur'); in the smallest bronchi, where the air has to force its way through narrow channels, it is more of a sipping, hissing, or whizzing nature (= *v* or *f*, 'vesicular murmur'). In the superficial respiration (of grown-up men) the character of the murmur becomes indeterminate; in like manner regular expiration produces an indistinct weak murmur.

Rhythm and Liberation of the Respiratory Movements.

The movements of inspiration and expiration can be produced at will. Ordinarily, however, they are involuntary, and have a certain rhythm and a certain intensity or depth.

We are able at will to vary both, in any manner we like; but total cessation is only possible for a very brief period of time. The medium frequence of respiration in an adult is 18 per minute.

The respiratory movements are increased in frequency in the very young and the very old, in the female, at high temperatures, during muscular effort, during digestion, with emotions, and after a temporary suppression of respiration, these agencies being the same as cause an increased frequency of pulse. In general we have in every condition one respiration to four heart's contractions. The influence of the passions affects not only the frequency but also the depth and the form of the respiratory movements; the latter producing thereby sometimes characteristic sounds or murmurs in the tubes which conduct the air to the lungs. To this category of characteristic sounds belong: *sobbing*, when the inspirations succeed each other quickly; *sighing*, when a deep inspiration is followed by a forced expiration; *yawning*, when there is slow and prolonged inspiration while the mouth is kept spasmodically opened; *laughing*, where there is a jerking, interrupted expiration; &c.

The impulse to the involuntary rhythmical respiratory movements proceeds from a circumscribed spot of the medulla oblongata, which is situated at the place of origin of the pneumogastric and spinal accessory nerves (Chap. XI.): the destruction of this spot suppresses at once all respiration, and is therefore fatal ('*Nœud vital*,' Flourens). From this spot the diaphragm is acted upon through the phrenic nerves, and the other inspiratory muscles through the external thoracic nerves; expiration also, as far as muscular forces are concerned in it, is under its influence. The rhythm of the excitations of the respiratory centre is influenced by certain fibres which run in the course of the pneumogastric, and which are in a constant state of irritation. There are two kinds of these fibres: the one kind are accelerating; the other, which the pneumogastric receives from the Ramus laryngeus superior (Rosenthal), or according to other authors (Pflüger and Burkart, Hering and Breuer) from other nerves, particularly the Ramus laryngeus inferior, are retarding or inhibitory. Ordinarily the excitation of the former (the accelerating) fibres predominates; for after division of one or both vagi (in the neck) the respiratory rhythm becomes slower (Traube): on artificial irritation also of the central end of the divided vagi, the excitation of accelerating fibres usually overbalances the other (the inhibitory), respiration in consequence becoming quicker: if the irritation is stronger

still, it becomes tetanic, *i.e.*, the diaphragm remains in a state of contraction—inspiration (Traube).   At times, however, we have the opposite effect on strong irritation, namely, the arrest of the diaphragm in a state of relaxation—expiration : this is particularly the case on the fatigue of the nerves—the result being due to the fact that the inhibitory fibres do not so quickly become exhausted (Burkart).   On excitation of the regulator-fibres the respiratory movements become deeper or more superficial in the same ratio as they become slower or quicker, so that the activity of the medulla oblongata remains nearly the same, though it is differently distributed : after section of the vagi, at least, the inspired quantities of gas are on the whole not less (Rosenthal), and the gaseous exchange, at all events at the commencement, is not altered (Voit and Rauber). The inspiratory muscles not in action before irritation of the accelerating fibres, are not affected by the irritation, which suspends also the action of those expiratory muscles which happened to be in action before.   On the other hand, with the increasing irritation of the inhibitory fibres, the expiratory muscles will at last come into play (Rosenthal), after the inspiratory movements have ceased.

The accelerating and inhibitory fibres belong to the class of regulator-nerves (for details see Chap. XI.).   Different views have already been expressed about the mode in which this regulation is set in motion peripherally during life (Rosenthal, Sklarek, Hering and Breuer).   The state of distension of the lungs seems to act mechanically as an excitant of these fibres (Rosenthal), expansion, on the one hand, exciting the inhibitory fibres, which act as expiratory fibres; and contraction, on the other, exciting the accelerating, which act as inspiratory, fibres; in this way there would be a sort of self-regulating mechanism presiding over the movements of respiration (Hering and Breuer) : the presence of regulator-fibres in the laryngeal nerves also shows that the larynx takes part in this regulation (Sklarek).

Irritation of the mucous membrane of the nose causes for some time an arrest of respiration during expiration ; this effect is brought about not by the olfactory nerve, but by the trigeminus (Hering and Kratschmer). A similar arrest in expiration follows the irritation of many cutaneous nerves, as, for example, the irritation of the cutaneous nerves of the chest on plunging into water (Schiff, Falk).

The exciting cause of the respiratory movements, of which more will be said further on, may either act directly on the medulla oblongata (Rosenthal) or on the terminations of the

centripetal nerves going to the medulla oblongata (Rach, v. Wittich), in which latter case respiration would be a *Reflex act.* The decisive experiment, namely, to determine whether all respiratory movements cease after the separation of the medulla oblongata from all its centripetal fibres, has been repeated by both sides with different results. It is, therefore, not possible to come to a decision on this point, as the other experiments carried out to support these two views do not agree among themselves.

The exciting cause itself consists in the presence of a certain amount of oxygen and carbonic acid in the blood. The following facts prove that this condition of the blood causes the respiratory movements :—1. The respiratory movements can be totally arrested ('*Apnœa*') if, either by a forced artificial respiration (by blowing air into the lung) or by voluntary forced breathing, the blood becomes saturated with oxygen and poor in carbonic acid. 2. Respiration becomes stronger, and the more accessory muscles take part in it ('*Dyspnœa* :' see Appendix), the poorer in oxygen and the richer in carbonic acid the blood is: as *e.g.* on the entrance of air or fluid into the pleural cavities, causing a collapse of the lungs, or when by inflammation, &c. the lungs are made unfit for respiration. The first respiratory movement in the fœtus is in like manner caused by interruption of the respiration carried on through the placenta, which causes a sudden deficiency of the oxygen in the blood, while the carbonic acid accumulates (Schwartz). 3. The same effect will be produced if this alteration in the composition of the blood takes place only locally in the vessels of the medulla oblongata ;[1] this happens, *e.g.*, on stagnation of the blood in these vessels, as after ligature of all arteries going to the brain (Kussmaul and Tenner, Rosenthal) or on preventing the return of venous blood from the brain (Hermann and Escher), whereby the blood becomes poorer in oxygen and richer in carbonic acid.

A very great deficiency of oxygen destroys the *excitability* of the medulla oblongata, and no irritation whatever, not even

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[1] This, however, is no criterion for the determination of the question whether the respiratory movements are a reflex act or not ; for the advocates of the first view will explain these results by holding the blood of the medulla oblongata to exert an influence in the production of the reflex action.

a large surcharge of carbonic acid, will again start respiration. This condition is called ' *Asphyxia* ' (see Appendix).

As almost all the conditions which increase the amount of carbonic acid in the blood are associated with a decrease in the quantity of oxygen, it is difficult to decide whether the want of oxygen or the accumulation of the carbonic acid forms the real 'liberating agent' for the respiratory movements. For the present it will be best to look upon both conditions as constituting the 'increased venosity' or 'dyspnoeic quality' of the blood (Hering). It is proved that respiration and dyspnœa may be caused by both a deficiency of oxygen without accumulation of carbonic acid (as in the respiration or artificial inflation of the lungs by indifferent gases free from oxygen, H, N, N_2O) (Rosenthal), and also by an accumulation of CO_2 without any deficiency of the O (as in the respiration of air which is rich in CO_2 without being poor in O) (Traube). The argument that in the first case also there is in reality an accumulation of CO_2, because the indifferent gases cannot expel the CO_2 from the blood as completely as O does (compare p. 153), and that therefore in both these cases the CO_2 is really the excitant (Thiry), is refuted by the consideration that the respiration of nitrogen causes no accumulation of CO_2 in the blood (Pflüger). We must therefore conclude (Dohmen, Pflüger) either that a deficiency of oxygen by itself, and likewise an accumulation of carbonic acid by itself, may excit the respiratory centre, or (Hermann) that if the CO_2 is alone the exciting cause, its action is the less powerful the larger the amount of O present, just as the action of strychnia, for example, is prevented when the blood is saturated with oxygen : see Chap. XI.

In apnœa the amount of O presented is increased in arterial and diminished in venous blood (Ewald) ; the latter condition is probably produced by a diminution in the velocity of the blood-current in consequence of the great decrease of the arterial blood-pressure (Pflüger).

The phenomenon of Cheyne and Stokes is a peculiar case of abnormal regulation of the respiratory movements : In patients suffering from cerebral and cardiac affections there occurs sometimes an intermittence of respiration; after each pause the respiration increases till dyspnœa is produced, when it gradually sinks again till the next pause. As an explanation it is stated (Traube) that when the excitability of the respiratory centre is diminished, a considerable increase in the venous state of the blood is required each time in order to excite it; the powerful respirations which eventually appear will, however, again considerably diminish the venous state.

APPENDIX TO CHAPTER IV.

CONSEQUENCES OF A DEFICIENCY OF OXYGEN.

IF by any means the access of oxygen to the blood be prevented altogether, or the quantity entering be diminished in an important manner; or if the oxygen which already exists in the blood be expelled from it or removed in any other way; a group of phenomena can be observed, which ultimately end in death (asphyxia, suffocation).

The oxygen which exists in chemical combination in the blood can be expelled from it by the inhalation of carbonic oxide (p. 46); further, the oxygen of the blood can be removed by substances which unite with it, as, *e.g.*, sulphuretted hydrogen. The circumstances which, according as they are in full or partial operation, check or altogether put a stop to the oxygenation of the blood, are the following : 1. A want of oxygen in the medium breathed (*e.g.*, prolonged respiration in a limited space of air, respiration in a vacuum or under water). 2. In the foetus, the separation of the placenta or closure of the umbilical vessels before birth. 3. Interruption to the cutaneous or pulmonary respiration, the former by varnish being applied to the skin (p. 150), the latter by closure of the air-conducting passages. The closure may be due to external causes, as when pressure is applied from without, in strangulation, or to internal causes, such as the following : spasmodic closure of the glottis; obstruction caused by foreign bodies or tumours; accumulation of morbid products, as mucus, in the bronchi; collapse of the lungs by the entrance of air or water into the pleural cavities (pneumothorax, pleuritic exudations); partial destruction of the lungs (as in phthisis); cessation of the respiratory movements; and, lastly, embolism of the pulmonary artery.

When placed in a chamber in which the air is rarefied, warm-blooded animals die before the whole of the oxygen has been consumed, in consequence of the evolution of gas within the blood, which leads to disturbance of the circulation (Hoppe-

Seyler). In compressed air death ensues in consequence of the elimination of carbonic acid being hindered (Bert).

With the impoverishment in oxygen which the blood undergoes under the above-mentioned circumstances, there is generally also an increase in the carbonic acid of that fluid, and these changes in the gases of the blood, as before said, at once cause the respiratory movements to become slower and deeper, under the influence of the *accessory muscles of respiration* (p. 162); this change in the respiratory movements constitutes *dyspnœa.* Dyspnœa is a regulating act, for in the majority of cases (unless when there is a complete absence of oxygen in the respiratory medium, or when the passage of oxygen to the alveoli is quite impossible) it leads to an increase in the quantity of oxygen contained in the blood, and then itself ceases.

If the impoverishment in oxygen proceeds further, general spasms of all the muscles of the body set in (clonic convulsions); the centre which presides over these is situated in the medulla oblongata, so that we must suppose that the stimulus which leads to normal respiration, if it be increased beyond a certain degree, exerts its action not only on the respiratory, but on neighbouring centres which were normally less irritable. Later on a contraction of the muscular coats of blood-vessels occurs which exerts an action upon the heart (see p. 77). This spasm of blood-vessels is an intermitting one (Traube), and follows the same rhythm as governs the rudimentary spasms of respiration, which are perceptible even at this stage. (Hering: compare Chapter XI.)

The spasms also occur when the flow of blood to the head is cut off, by ligaturing the carotid and vertebral arteries, and also when an animal loses large quantities of blood (Kussmaul and Tenner); when produced in these ways the spasms have been designated ' anæmic:' their true cause is, however, in all cases, the presence of stagnating blood in the capillaries of the brain,—that is to say, of blood which is poor in oxygen and rich in carbonic acid—and they can therefore be produced by preventing the return of venous blood from the brain (Hermann and Escher). Even in the experiment of Kussmaul and Tenner, dyspnœa precedes the spasms (Rosenthal). After hæmorrhage we can readily conceive how stagnation of blood in the vessels

of the brain may result in consequence of insufficiency of the propulsive power : it would, however, in this case, be just as easy to suppose that either the want of oxygen or the increase in the quantity of carbonic acid might act as excitants of the substance of the brain.

If the want of oxygen proceeds still further, the irritability of the nerve-centres, which requires for its maintenance a certain supply of oxygen, ceases, and the strongest irritants cannot occasion either movements of respiration or spasms, which, therefore, are in complete abeyance : this condition, which must not be confounded with ' Apnœa' (p. 169), is called ' Asphyxia.' When it has set in, the heart very soon ceases to beat, and death (by suffocation) occurs.

In the state of asphyxia. so long as the heart continues to beat, recovery is still possible (except in cases where the blood has been saturated with carbonic oxide) by distending the lungs with oxygen (artificial respiration). The phenomena which were previously referred to as occurring necessarily during the production of asphyxia then recur, but in inverse order, viz. first of all spasms, then dyspnœa, then normal respiration, and lastly, if air be very energetically introduced, apnœa.

In the dead bodies of asphyxiated animals no difference exists between arterial and venous blood. All the blood of the body is of a dark red colour (this is not the case when death has resulted by the action of carbonic oxide); no oxygen capable of being removed by the usual means is present, and the blood exhibits, when it is examined with the aid of the spectroscope, the absorption band of reduced hæmoglobin (p. 46); the quantity of carbonic acid is, on the other hand, increased, although not to such an extent as would correspond with the diminution in the quantity of oxygen. The quantity of combined carbonic acid and of nitrogen remain unchanged (Setschenow).

If the blood of asphyxiated animals be shaken with oxygen, a portion of the latter is at once consumed, carbonic acid being formed, apparently in consequence of the presence of easily-oxidized (reducing) substances.

When the deficiency of oxygen persists for a long period, but in a moderate degree, *e.g.*, in cases of partial destruction of lung, in one-sided pneumothorax, the requirement of oxygen and its supply become adjusted : in consequence, those functions of the body which are associated with oxidation become corre-

spondingly diminished, and the body becomes cooler, more flaccid, the respiratory movements become more rapid. Continuous deficiency of oxygen makes itself perceived by the darker colour of the blood, which, aided by a relaxation of the smaller arteries, causes the blue tint presented by the lips, and other mucous membranes (Cyanosis).

Respiration of Foreign Gases.

In warm-blooded animals the supply of oxygen cannot, consistently with the preservation of life, be dispensed with even for the shortest time ; still the oxygen may be mixed with other innocuous gases (hydrogen, nitrogen), as in the atmosphere.

The statement that nitrous oxide (laughing gas) could replace oxygen for considerable lengths of time (H. Davy) has not been confirmed ; pure N_2O causes dyspnœa and asphyxia to occur at once in warm-blooded animals; but in man the former is not perceived, owing to the intoxication it produces (Hermann).

The other gases may be classified, in so far as their action on living beings is concerned, in the following manner :—

A. *Indifferent Gases.*—These can, when mixed with oxygen, be respired for an indefinite time without injurious consequences. 1. Nitrogen ; 2. Hydrogen ; 3. Marsh gas. If inhaled alone, they occasion dyspnœa, spasms, and asphyxia.

B. *Irrespirable Gases.*—These can only be respired when very small quantities of them are mixed with other gases, because in more concentrated states they induce, by reflex action, spasm of the glottis. To this group belong :

a. *Gaseous acids.*—1. Carbonic acid, which being the weakest acid is in the least degree irrespirable, and can therefore be respired in a tolerably concentrated form ; when it is respired through tracheal fistulæ it exerts a poisonous action (it therefore has a place under Group C). 2. Hydrochloric acid ; 3. Hydrofluoric acid ; 4. Hyponitric acid ; 5. Sulphurous acid, &c.

b.—*Gases which form acids*: 1. Nitric oxide (NO), when mixed with oxygen at once forms hyponitric acid ($NO + O = NO_2$), and would prove poisonous could it reach the blood (consult Group C). 2. Phosgene gas (chloro-carbonic oxide), $COCl_2$ (p. 23) when it comes in contact with water at once splits into carbonic acid and hydrochloric acid ($COCl_2 + H_2O = CO_2 + 2HCl$).

3. Chloride of boron (BCl_3) in contact with water gives boracic and hydrochloric acids. 4. Fluoride of boron ($B Fl_3$) in contact with water gives boracic acid and hydroborofluoric acid. 5. Fluoride of silicon ($SiFl_4$) under similar circumstances gives silicic acid and hydrofluosilicic acid, &c.

c. *Alkaline gases.*—1. Ammonia; 2. Substitution derivatives of ammonia, as methylanium, &c.

d. *Gases capable of forming substitution compounds or of exerting an oxidizing action.*—1. Chlorine; 2. Fluorine (?); 3. Ozone.

. Irrespirable gases can be introduced, through tracheal fistulæ, into the lungs of the lower animals; they generally exert a strongly destructive action upon these organs. Spasm of the glottis is therefore a protective act, and it ceases after the vagi had been divided.,

C. *Poisonous Gases.*—These can be respired, but being taken into the blood they lead to injurious or fatal consequences.

This group can be subdivided as follows :

a. *Reducing Gases.*—These become oxidized at the expense of the blood, the oxygen of which they remove ; in this manner they lead to the phenomena which are caused by a deficiency of
• oxygen (p. 171), dyspnœa, convulsions, and asphyxia. 1. Sulphuretted hydrogen, H_2S, is oxidized in the blood, H_2O and S being formed. As soon as the blood has been freed from oxygen, its hæmoglobin is decomposed, with the formation at first of a body like hæmatin, then of a green substance: these actions do not really go on in warm-blooded animals ; for before time for their production has elapsed, death results in consequence of the removal ,of oxygen (Hoppe-Seyler, Kaufmann and Rosenthal). 2. Phosphuretted hydrogen (PH_3) is oxidized in the blood, phosphoric acid and water being formed (Dybkowski). 3. Arseniuretted hydrogen, AsH_3, and 4. Antimoniuretted hydrogen, SbH_3, appear to exert a similar action to the preceding. 5. Nitric oxide gas, NO, appears at first to, act as a reducing agent (Hermann): it is, however, irrespirable. 6. Cyanogen, C_2N_2, also exerts a reducing action on blood, soon, however, leading to further changes (Rosenthal and Laschkewitsch).

b. *Gases which expel Oxygen.*—These expel the oxygen from its combination with hæmoglobin, and then form a more stable

and a brighter coloured red compound; they also occasion the phenomena which are characteristic of a deficiency of oxygen.

1. Carbonic oxide gas, CO (compare p. 46). If the blood be not completely saturated with CO, recovery is possible, for the oxygen yet present in blood cán oxidize the CO and produce CO_2 (Pokrowsky).

2. Nitric oxide likewise forms a stable compound with hæmoglobin (Hermann): in consequence of its irrespirable nature, it cannot in reality exert this action.

c. *Intoxicating gases, which, when inhaled with oxygen, occasion loss of consciousness and anæsthesia :—*

1. Nitrous oxide gas, N_2O (H. Davy);

2. Chloride of Methyl, CH_3Cl (Hermann);

3. Carbonic acid, CO_2, leads to a series of complicated phenomena, of which some have already been referred to at pp. 79, 170, and 174; it further induces a kind of stupor (Narcosis); the cause of these phenomena is not yet fully understood.

d. *Poisonous Gases, the mode of action of which is not known.*—To this class belong the majority of the remaining gases, which have as yet been very slightly investigated.

CHAPTER V.

THE EXCHANGES OF THE MATTER OF THE BLOOD.

THE causes of loss and of gain to the blood (expenditure and income) having been considered in the three preceding chapters, the means by which the blood and its constituents remain absolutely and relatively constant must now be discussed.

That under normal conditions of life the income and expenditure of the blood almost exactly balance is proved by the very constant amount (tension) and composition of the blood. Slight fluctuations occur, it is true, even in the normal state, but these are only temporary; an example of such occurs during the time of digestion, when the income decidedly preponderates in amount over the expenditure. It is not yet possible to strike a balance between the income and expenditure of the blood, seeing that as yet it is impossible, even approximately, to ascertain the exact amount of either.

Changes having their seat in the Blood Corpuscles.

It is possible to conceive of changes in the chemical constituents of the blood corpuscles occurring without any simultaneous morphological change. Many facts, however, which will be subsequently referred to, indicate that continually red blood corpuscles are being destroyed, whilst new ones originate. Other facts indicate that the new red corpuscles take their origin in colourless ones.

Tolerably accurate facts are forthcoming in reference to the origin of the latter (the colourless); but far less is known of the place and nature of the transition of colourless into red corpuscles, or at least as to the exact mode of transition.

1. The colourless blood corpuscles are identical with the lymph cells, but probably originate in new-born animals

almost entirely in the *lymphatic glands* and *follicles* (as well as in some apparently similarly constructed organs, as the *thymus* and *thyroid glands*), in the *spleen* and the *marrow of bones* (Neumann). The cells which are formed in the first-named organs are poured into the blood with the lymph; those which originate in the spleen and the marrow of bones, on the other hand (with the exception of those from the splenic follicles, which appear to belong to the lymphatic system), are directly mixed with the blood, in part after being already converted into red corpuscles.

The lymphatic glands and follicles have already been alluded to.

The thymus gland, an embryonic thoracic organ which grows very slowly after birth, and which later in life completely disappears, consists, according to the most recent researches, of *alveoli*, which correspond completely to the lymphatic alveoli and follicles; it also contains products of degeneration (fat cells, amyloid bodies, &c.). Its structure, and the abundant lymphatic vessels supplied to it, lead one to look upon the thymus as an organ similar to the lymphatic glands. In the thyroid body also, according to some (Jendrassik and, in the case of the frog, Toldt), lymphatic alveoli occur as normal constituents. The cysts which are found in the thyroid filled with colloid masses and crystals of unknown nature, are looked upon as due to a *degeneration*, whilst other vesicles, filled with fluid and lined with epithelium, are looked upon as the normal constituents.

The supra-renal capsules belong to a class of organs of like structure; the areolar tissue of these organs is filled with cells which, by some, are considered identical, or almost identical, with nerve-cells. Concerning their function nothing is known. In consequence of their richness in nerve-fibres and in the above-mentioned cells, some look upon them as a variety of sympathetic ganglia. Others consider them to be connected with the formation of pigmentary matters. In a certain anomalous pigmented condition of the skin (bronzed skin) the supra-renal capsules are diseased (Addison), and a violet substance can be extracted from them (Holm).

The structure of the spleen is similarly involved in obscurity (on this subject consult histological text-books). According to the now most generally received conception, the following propositions may be stated:—

1. The *Malpighian vesicles*, which are situated on the sides of the finer arterial twigs, are to be considered as lymph follicles (Gerlach); these form circumscribed thickenings of the arterial wall, and may be considered as simple deposits of colourless (lymph) cells between the separated layers of the adventitia; in many animals this alveolar thickening is not circumscribed, but is more uniformly distributed over the arterial wall (W. Müller).

2. The *splenic pulp* consists, according to some (W. Müller, Frey), of spaces which are quite similar to the alveoli of the lymphatic glands, except that in the splenic pulp the blood-vessels play the same part as the lymphatics in the glands, *i.e.* the capillaries open into the alveoli, which are

filled with lymph cells, and from the alveoli originate the veins. The constituents of the blood thus become mixed with the lymph corpuscles which are there. Besides the red and colourless cells, numerous transition forms between the colourless and coloured blood corpuscles occur in these spaces, and in addition coloured cells and nuclei, which are held to be red blood corpuscles undergoing retrograde changes; these nuclei are in part free, in part enclosed in cell-like masses. Others (Billroth, Kölliker, Kyber, Wedl) look upon the blood-vessels as forming a system of perfectly closed paths, and explain the apparent admixture as artificial. The splenic pulp has an acid reaction, and, in addition to all the blood constituents, it contains numerous products of oxidation : uric acid, hypoxanthine, xanthine, leucine, tyrosine, inosite, volatile fatty acids (formic, acetic, butyric acids), and lactic acid. It contains, in addition, numerous pigments, an albuminous substance containing iron, and (a fact most worthy of notice) many compounds of iron. The venous blood of the spleen contains an extraordinary number of colourless cells (1 to 70 red, Hirt), and the coloured cells found in it are distinguished from others by their smallness, by their being only slightly flat, by their great resistance to the action of water and by their not having a tendency to arrange themselves into *rouleaux* ; these characters are considered to be evidences of their recent formation. In addition, the venous blood of the spleen, like the splenic pulp, contains many transitional forms.

Extirpation of the spleen does not necessarily cause death. The function of this organ appears to be capable of being replaced by other lymphatic organs (lymphatic glands, marrow of bones), which enlarge under the circumstances.

The *marrow of bones* contains, in an areolar network, which is quite similar to that of the lymphatic glands, numerous colourless contractile cells, which entirely agree in characters with lymph cells, and, in addition, also transitional forms between these and red blood corpuscles (Neumann, Bizzozero). The way in which these cells pass into the blood-vessels is not yet ascertained.

The formation of lymph cells in all these organs is, according to the more recent investigations, a process which in its nature agrees with the origin of connective tissue corpuscles.

The analogous colourless contractile corpuscles, which are able to wander actively from place to place, and are found in the canal-system of the connective tissue, in the lumen of the lymphatic vessels which originate from this tissue, in the expanded canalicular system of the lymphatic glands and follicles, and, lastly, in the analogous spaces in the spleen, are, we must surmise, constantly being propagated (by a process of fission), so as continually to replace those which pass into the blood (Virchow, v. Recklinghausen).

These views are supported by numerous facts, and, amongst others, by the following :—the presence of lymph cells in lymph which has not yet passed through any lymphatic gland or follicle; further, the pathological formation of lymph cells from undoubted connective tissue cells in leuk-æmia, a disease in which also the formation of lymph cells in the lymphatic glands or in the spleen (sometimes also in the *medulla ossium*), is morbidly increased; lastly, according to some writers, the formation of pus cells exactly similar to lymph cells by a multiplication of connective tissue cells (Virchow, C. O. Weber, Rindfleisch, Stricker); this is, however, denied by others (Cohnheim).

The new formation of colourless blood cells appears to be thus shared by several formative organs, so that one can replace or supplement the other. This conclusion is drawn from the fact that extirpation of any of these organs (spleen, thymus, lymphatic glands, &c.) is followed by no bad consequences to the body, but is compensated for by a vicarious enlargement of the remainder. When, however, several of these organs are extirpated at the same time, life is endangered.

The formation of blood corpuscles in the embryo is quite different from the process which goes on during extra-uterine life. The first blood cells originate with the blood-vessels, inasmuch as the innermost layers of the rows of cells which form the latter are directly converted into blood cells and by fission give rise to new ones (Remak, Kölliker). Later on, as soon as the liver is formed, the formation of blood corpuscles is transferred to this organ (E. H. Weber, Kölliker); nevertheless, the process is not clear, nor is the fact itself altogether certain.

Some (Lehmann, Funke) attribute to the liver, during the whole course of life, the function of forming new blood cells, relying chiefly on the rich-ness of the blood of the hepatic veins in colourless cells and in newly formed red corpuscles (similar to those of the splenic blood); nevertheless these observations permit of being otherwise interpreted (see below), and hitherto no follicle-like organs have been detected in the liver.

2. The conversion of colourless into red blood corpuscles appears to occur generally throughout the blood, although it has only been directly demonstrated in the spleen, the venous blood of which contains numerous transitional forms, and in the marrow of bones. The chemical transformation upon which it depends, viz. the origin of hæmoglobin, is unknown; it is affirmed that this substance crystallises with peculiar readiness in the newly formed red corpuscles (Funke). Hæmoglobin appears to originate under the influence of oxygen, inasmuch as lymph and organs containing lymph are seen to assume a red tint on exposure to air (Virchow, Friedreich). The morphological

change consists, according to the received view, in a disappearance of the nucleus, which is followed by a general flattening of the cell, which becomes red; at the same time the corpuscle appears to permit of diffusion taking place into it more and more readily. The young cells, which have just become red, as they are found in splenic and hepatic venous blood, swell but slightly in water and are not as decidedly flattened as the ordinary, older, blood corpuscles, which are easily destroyed by water, are disk-shaped, and are also larger.

In the frog the passage of colourless into red blood corpuscles can be directly observed to occur in blood which has been drawn from the body (v. Recklinghausen). The transitional forms which originate in this process are also observed in the circulating blood.

A portion of the colourless cells may possibly not be converted into red, but be destroyed by a process of fatty degeneration (Virchow).

3. Little is yet known in reference to the destruction of the red corpuscles. It may be suspected to occur wherever colouring matters originate, as it is probable that these all are derived from blood colouring matter which has been liberated, therefore especially in the spleen, the liver, the kidney, &c.

Most probably a considerable destruction of red blood corpuscles takes place in the spleen and liver.

In the spleen, if actually the blood is (according to the previously enunciated views) obliged to filter between the colourless cells of the alveoli, many of the cells which penetrate therein with the arterial blood, are probably retained. The actual occurrence of such a retention is rendered probable by the following facts :—the traces of substances which are due to the destruction of coloured cells ; the shrivelled cells caught in the act of retrograde metamorphosis ; the pigmentary matters and ferruginous compounds and perhaps also the oxidation products ; further, the circumstance that the venous blood of the spleen contains only colourless and young red blood corpuscles. The cells which appear to contain blood corpuscles seem to originate by colourless contractile cells taking into themselves red blood corpuscles.

A destruction of red blood corpuscles in the liver appears probable from the fact that the salts of the bile acids possess the power of dissolving the red corpuscles, as well as from the fact that bile pigment is formed; further, from the extremely slow flow of blood through the liver, and lastly from the poverty of the blood of the hepatic veins in the older red corpuscles. The latter, like the splenic venous blood, contains, as has been already mentioned, only young coloured, and many colourless, cells (Lehmann) ; from this we may in nowise conclude that a new formation of blood corpuscles takes place in the liver, for the new cells of the splenic vein are conducted to the liver by the portal vein. If we suppose that the 'old' red cells carried by the other radicles of the portal vein are in part or wholly

destroyed in the liver, the blood of the hepatic veins must naturally contain a greater number of new elements than the portal blood.

Consequently it appears that a fractional portion of the blood contained in the cœliac and mesenteric arteries loses its red corpuscles, in part directly in the spleen and liver (hepatic artery), in part in the liver (portal vein) only after the stomach and intestines have been supplied. Even in the marrow of bones where pigment and cells containing blood corpuscles are found (Bizzozero; according to Neumann only in pathological conditions) a destruction of red blood corpuscles must occur (Bizzozero).

Exchanges of the Chemical Constituents.

Even less is certainly known in reference to the exchanges of the chemical than of the morphological constituents of the blood. We are acquainted, it is true, in a general manner, as has been explained in the last three chapters, with the constituents which the blood receives and excretes, but we only know approximately the magnitude of this exchange, nor do we know in what manner it is distributed over the various seats of exchange. Further, we know almost nothing on the question as to whether chemical changes of its constituents go on within the blood itself.

The fact that in fresh blood, which contains oxygen, but which is free from carbonic acid, either no carbonic acid or only a mere trace of it is formed, is opposed to the view that oxidation takes place within the blood. On the other hand, it is usually assumed that the fibrinogenous substance originates either within the blood or in the lymph, from other albuminous substances; but even this is no certain fact, for it is possible that it may be taken up, already formed, from some organ. It is further ascertained that certain easily oxidisable substances, as lactate or caprate of sodium, and glycerin (on the contrary not sugar, or formiate, acetate or benzoate of sodium), when injected into the blood are readily burned, and also when they are made to pass, mixed with blood alone, through any organ; it is, nevertheless, not known whether this process of combustion occurs in the blood itself (Ludwig and Scheremetjewsky).

The exchanges amongst the chemical constituents of the blood which take place during secretion and absorption may shortly be summed up as follows.

1. The gaseous exchanges of the blood have already been systematically discussed in Chap. IV.

2. The inorganic constituents are continually being absorbed in large quantities from the digestive apparatus and from paren-chymatous juices, and similarly are being given out to paren-chymatous juices and secretions, water besides passing in the process of cutaneous or pulmonary respiration, directly into the atmosphere.

The constancy in the proportion of the inorganic constituents of the blood is maintained by the following arrangements.

A. Water. A diminution of the water of the blood must so influence the exchanges due to diffusion, that, on the one hand, less water is given up by the concentrated plasma to the paren-chymatous juices and secretions, whilst on the other hand more water is absorbed. Further, every diminution in the amount of water of the blood is accompanied by a diminution of the volume of that fluid, and therefore by a diminution of the pressure of blood in the vessels, so that less water is given up even in pro-cesses of filtration. This effect is most marked in the diminu-tion of the water contained in (and therefore in the amount of) those secretions which are poured outside the body, such as the urine and sweat. In the tissues themselves this effect of a diminished blood pressure is noticeable only in their diminished turgescence.

Finally, local deficiencies in the amount of water in certain tissues give rise to specific sensations, which lead to an increased quantity of water being taken with the food (Thirst, Chap. VI). Conversely, an excess of water in the blood naturally leads to increased excretion by filtration and diffusion, which again is manifested by an increase in the quantity of urine and sweat, and by a cessation of thirst.

Concerning the distribution of water in the body, see Chap. VI.

B. Salts. Even changes in the saline constituents of the blood must modify, as is easily intelligible, the diffusion-ex-changes of the blood in such a manner as to lead to an approxi-mate constancy in its saline composition as a whole. We do not, however, know by what means the amounts of the individual salts are maintained constant, or whether a mutual replacement occurs.

3. Organic constituents. As the forces in virtue of which or-ganic substances pass into and out of the blood are as yet quite

unknown to us, we cannot surmise the nature of the mechanism, analogous to that alluded to in discussing the inorganic constituents, which maintains them in an approximately constant quantity. We merely know that a continual introduction of organic alimentary substances takes place in consequence of certain mysterious sensations (hunger and thirst), the intensity of which varies with the wants of the system.

The receipt of organic substances into the blood occurs in part without any further change, when they are absorbed from the food without having undergone chemical changes; this is the case with many of the soluble organic constituents of food, with a portion of the soluble albumin, and, lastly, with a portion of the fat, which is absorbed into the blood in a state of simple emulsion.

The greater number of the alimentary constituents undergo, however, chemical changes in the process of digestion (Chap. III.), and the products of these which are absorbed, appear (after absorption) to undergo further changes before they are converted into constituents of the blood. These changes, which are in great part unknown, are expressed by the term 'assimilation.' The following processes of assimilation have been as yet approximately discovered :

1. Albuminous bodies, gelatin and allied substances are in part converted into peptones before absorption, and in part they are still further decomposed. Inasmuch as peptones cannot be detected in the juices or tissues (Lehmann, Hoppe-Seyler and De Bary) and do not pass into the urine (Fede), they must rapidly be converted into other bodies, presumably into albuminous bodies.

2. A portion of the fatty matters undergoes decomposition in the intestine, and being saponified, absorption of soaps occurs. Seeing that from soaps taken as food the corresponding fats are formed in the animal body, it is probable that the soaps which are formed in the intestine can, after absorption, be reconverted into fats (Radziejewsky).

3. Sugar, ingested as such or formed in the process of digestion out of starchy constituents of food, is, after absorption, converted into a starch-like substance (glycogen) in the liver (see the Appendix to this chapter).

Seeing that a portion of the albuminous bodies undergoes absorption without a previous conversion into peptones, some suppose that peptones are not reconverted into albumin, but, being burned up so as to furnish urea, are excreted.

The seat of these processes of assimilation is as yet unknown. Many suppose them to occur in the liver, in which organ especially the processes referred to under (3) are to be localised. These processes are, as a whole, synthetic, in opposition to the hydrolytic processes of decomposition which occur during digestion, and of which they are the exact reversals (another synthesis which goes on in the body, that of hippuric acid from glycocine and ingested benzoic acid, apparently occurs in the liver, Kühne and Hallwachs). The process by which the alimentary principles are split up in the intestine (the products of decomposition being, after absorption, employed in synthetic processes, partly in the re-formation of the original substances), is of use from two points of view (Hermann): in the first place, the products of decomposition are in general, on account of their smaller molecules, more easily absorbed than the original substances; in the second place, the products of decomposition furnish a more simple formative material, which alone renders possible the synthesis of the numerous substances which the body requires.

The majority of the complex substances which the body requires must necessarily first arise within it by synthetic processes. As the introduction, with the food, of ready-made hæmoglobin, of undecomposed muscular substance, &c., is impossible, because these bodies are partly decomposed spontaneously, and partly in the alimentary apparatus, it follows that assimilation must consist of syntheses (Hermann).

In reference to hæmoglobin it has been ascertained that its quantity in the blood is increased by an albuminous diet (Subbotin).

As little is known of the nature of the processes which are concerned in the supply of organic constituents from the blood to the tissues, as of those concerned in the introduction of organic constituents into the blood.

Constancy of the Amount of Blood in the Body.

The constancy in the amount of the blood in the body naturally depends upon the constancy of the different constituents of the blood. As water is by far the principal ingredient

of the blood (forming about 80 per cent. of its weight), and as the volume of blood is almost equal to that of the water which it contains, it follows that in the preservation of the constancy of the volume of blood, the constancy in the quantity of water is of greatest importance; the mechanism concerned in the preservation of the latter has been already discussed. Actually, after great losses of blood, its volume is very soon restored, for, under the diminished blood-pressure, less water is given up to the tissues and to the secretions and more is absorbed, whilst, in addition, increased thirst leads to increased introduction of fluids.

APPENDIX TO CHAPTER V.

FORMATION OF GLYCOGEN AND SUGAR IN THE TISSUES.

In many of the animal tissues there occurs a starch-like, or, more correctly, a dextrin-like substance, named *glycogen*, which is very easily converted into sugar by the same means as effect the conversion of starch. This substance occurs principally in the liver (Bernard, Hensen), in muscles (Macdonell, O. Nasse), in nearly all the tissues of the embryo and of its appendages (Bernard), as well as in the tissues of young animals, and in newly-formed pathological formations (Kühne).

Glycogen appears to occur frequently in small organisms, *e.g.* it is found in the Ascaris lumbricoides, and principally in its muscles (Foster). Sugar-forming (glycogenic) substances, which more or less closely resemble the glycogen of the liver, occur also in the brain (Jaffe), in the muscles (dextrin, Limpricht), in many glands (Kühne, Brücke), in blood (Brücke), &c.

Glycogen is obtained from liver by pounding the perfectly fresh organ in sand and water at 100° C., acidulating the fluid so as to completely decompose the alkaline albuminates, filtering and boiling the residue with fresh portions of water until the filtrate is no longer opalescent. The united precipitates are evaporated to half their bulk and precipitated with alcohol, by which the glycogen, mixed with some glutin, is precipitated in white flakes; from the latter it is purified by boiling with caustic potash, neutralising and precipitating with alcohol.

.It is more easily obtained free from nitrogenous contaminations by pre-

cipitating the aqueous extract of liver by means of a solution of iodide of mercury in iodide of potassium previous to throwing down the glycogen by means of alcohol (Brücke).

Ferments which are capable of converting glycogen into sugar, are not only contained in the sugar-forming secretions (saliva, pancreatic juice) but also in the liver (Bernard), in the blood, and in almost all the tissues (v. Wittich, Lépine). The liver when removed from the body contains large quantities of sugar, which go on increasing as long as glycogen is present.

A question which has not yet been decided is whether the liver contains sugar during life. A perfectly fresh liver taken from an animal immediately after it has been killed contains, according to some (Bernard, Kühne), small but yet perceptible quantities of sugar, according to others (Pavy, Ritter, Schiff, Eulenburg), not a trace. A formation of sugar in the liver during life is further rendered probable by the fact that the hepatic venous blood of animals fed upon a diet containing neither starches nor sugars, is richer in sugar than the blood of the portal vein (Bernard, Tieffenbach); this continuous passage of sugar has been found to be associated with the presence of only a very small quantity of, or even with no sugar in the liver, whilst the very presence of sugar in the liver, and specially its presence in the blood of the hepatic veins, has been denied (Pavy, Ritter, Schiff).

Those who suppose that no sugar is formed in the liver during life, argue either for the presence of a sugar-forming ferment which is only formed after death or in pathological conditions (Diabetes) (Schiff), or suppose that the ferment being present is restrained from exerting its action by a kind of inhibitory influence of the nervous system (Pavy).

The pre-existence of such a ferment in the blood and tissues has lately been contradicted (Lépine, Plósz, Tiegel).

Blood exerts no action on glycogen unless its corpuscles have been destroyed (by the action of water, ether, &c.) so that probably the blood corpuscles generate the ferment at the very moment of their destruction (Plósz, Tiegel). It is worthy of observation in reference to this matter that probably a destruction of blood corpuscles is continually taking place in the liver.

The presence of glycogen in the liver depends very much

upon the food. Its amount is large in proportion as the latter is rich in carbo-hydrates (Pavy, Tscherinoff).

In warm-blooded animals which are starved glycogen disappears in the course of a few days, and reappears in large quantities after the injection of sugar into the intestine (Dock). The same result is produced by injections of glycerin (Weiss). Hence we must conclude that glycogen is derived in the liver from sugar, by the formation of an anhydride.

Another supposition, which has been investigated, considers other substances (proteids) to be the source of glycogen; glycogen is, however, easily further oxidized, if other easily-oxidized substances, such as sugar, are not present to keep oxygen from attacking it. In support of this is adduced the fact that even injections of glycerin into the intestine cause the liver to contain glycogen. In opposition to it, recent researches would show that sugar is not an easily oxidized substance (Scheremetjewsky); further, some other easily oxidized substances, e. g. sodium lactate, bring about no increase in the quantity of glycogen, and glycerin does so only when it is injected into the intestines, and not when it is subcutaneously injected (Luchsinger). Other kinds of sugar, as milk-sugar and levulose, furnish normal glycogen (Luchsinger).

The different kinds of sugar, and glycerin, which is closely allied to them, appear to be converted into glycogen when they are carried to the liver in the blood of the portal vein. In support of this it may be stated that sugar when injected into the portal vein does not appear in the urine, whilst it does so when it is injected into other veins (Schöpffer).

The destination of the glycogen of the liver is not accurately known. Those who believe that a formation of sugar takes place during life suppose that glycogen is converted into sugar, which is partly excreted and partly burned. Other possible hypotheses as to its destination are the following: that it is carried to other organs which contain glycogen (the muscles, the testicles) and is there consumed; further, that it is converted into other substances, e. g. into fats, &c.

Under certain circumstances an abundant excretion of sugar takes place through the urine—diabetes.

These circumstances are: 1. Pathological alterations the seat and nature of which are unknown to us (pathological

diabetes). 2. Injury of a limited space in the medulla oblongata, in the floor of the fourth ventricle (traumatic diabetes, Bernard). 3. The action of certain poisons, especially of curare. 4. The injection of very dilute salt solutions into the blood-vessels (Bock and Hoffmann). The cause of diabetes may be sought for: *a.* in a conversion (or increased conversion) of the glycogen of the liver or of other organs into sugar ; *b.* in a diminished conversion of ingested sugar into glycogen ; *c.* in a diminished destruction of sugar normally originating in the glycogen of the liver.

In pathological diabetes the sugar disappears, almost if not entirely, from the urine, when no carbo-hydrates are taken as food. Even puncturing the floor of the fourth ventricle (der Zuckerstich) induces no diabetes if the animals have, in consequence of starvation, livers free from glycogen (Dock).

In animals in which diabetes has artificially been induced, feeding with sugar does not, as it normally does, cause the liver to contain glycogen. Hence it follows that traumatic, and probably also pathological, diabetes depend upon the incapability of the liver to arrest the sugar which is brought to it, and convert it into glycogen, so that sugar passes unchanged into the urine, or accumulates in other organs. On the contrary, starved animals become diabetic under the influence of curare, even when no sugar is furnished to them (Dock) ; probably in this case the sugar is derived from a store of glycogen (possibly contained in muscles) which is converted into sugar.

The proximate cause of traumatic diabetes has lately been sought for in a paralysis of the blood-vessels of the liver (Schiff, Cyon and Aladoff).

The spot on the fourth ventricle the puncture of which occasions diabetes is possibly a portion of the vasomotor centre (Chap. XI.)

Even other injuries affecting the vasomotor supply of the liver, *e.g.* injury of the inferior cervical ganglion or of the nerves which proceed from it to the *ganglion stellatum*, occasion diabetes. On the contrary section of the splanchnic nerves, which probably lowers the blood pressure too much, does not induce diabetes (Cyon and Aladoff). It is indeed asserted that irritation of the splanchnic nerves causes diabetes (Gräfe). Even diabetes induced by curare may possibly be referred to a vasomotor paralysis.

From what has been previously stated vasomotor paralysis should, on the one hand, hinder the formation of glycogen from sugar, or should convert the glycogen (whether stored up in the tissues or newly formed) into sugar, by exciting a hitherto unexplained influence upon the development of the amylolytic ferment. When diabetes follows the injection of dilute saline solutions, the destruction of blood corpuscles may take a part in the formation of the ferment ; in these cases the ferment passes into the urine (Plósz and Tiegel).

CHAPTER VI.

EXCHANGES OF THE MATTER OF THE BODY, AS A WHOLE.

I. INCOME.

As has already repeatedly been said, the organism receives regularly from without :

1. Food, *i.e.* material for the repair of that which has been excreted either after undergoing oxidation, or in an unoxidized, unaltered condition.

2. Oxygen, for the oxidation of those constituents of the body capable of it. All that is to be said concerning the introduction of oxygen will be found in Chap. IV. Food, on the other hand, here requires a closer consideration.

Food.

The elements of food must in general be the same as those of the body, if they are to serve for the repair of the losses of the latter. Their introduction into the body in an isolated condition is, however, of no value for the purposes of nutrition, because in the case of some of them absorption into the blood is impossible, and in the case of others which are capable of absorption their elaboration into the chemical compounds which they are to repair is not practicable within the body. As a rule, therefore, chemical compounds alone are capable of use as food, and only in so far as they satisfy the following conditions :

1. The compound must be fit for absorption into the blood or chyle, either directly or after preparation by the processes of digestion (*i.e.* it must be ' digestible ').

2. It must replace directly some inorganic or organic constituent of the body ; or it must undergo conversion into such a constituent while in the body ; or it must serve as an ingredient

in the construction of such a constituent. Neither itself nor any of the possible products of its decomposition must be detrimental to the structure or activities of any of the organs of the body (such detrimental bodies are called ' poisons ').

Scarcely a single nutritious substance is taken into the body by itself, almost all being ingested, when mixed together in certain proportions found in nature and called ' Foods,' which are for the most part vegetable or animal tissues or portions of such tissues. These also are generally further mingled together by artificial means and prepared in various ways, partly to facilitate digestion and partly to render them more palatable.

In the preparation of nutritious material as foods, the most essential process is the addition of so-called ' spices,' that is to say, of substances possessed of such stimulating qualities as render them peculiarly fitted for inducing in a reflex manner the secretion of the alimentary juices (saliva, gastric juice, &c.). The commonest seasoning is salt, which, however, is, in addition, a nutritious body (see below). The preparation of food by boiling, roasting, baking, &c., has for its special object to assist the processes of digestion by anticipating certain of its stages, *e.g.* by dissolving what is soluble, by rendering capable of solution what is insoluble, by loosening the compacter portions, by breaking indigestible skins or husks, &c.

In consequence of what has been said above, all nutritious substances fall into two natural classes, both of which ought to be represented in the food. The first class, which serves for the repair of the unoxidizable constituents of the body, consists of the inorganic elements of food, essentially water and salts ; the second, destined to replace the oxidizable portions which are lost, and including therefore bodies which are themselves oxidizable, consists of the organic elements of food. The latter in common with all organic substances are derived immediately or mediately from plants ; for even the organic constituents of the animal body (forming ' animal food ') can be traced back to the vegetable kingdom, as carnivorous animals feed directly or at least in the last instance upon herbivorous animals.

Only a very small proportion of the various organic compounds of C, H, N, O, S, etc., which are formed in plants, really rank as nutritious substances, as many do not fulfil the previously mentioned conditions. The animal substances resulting from the assimilation of such of them as are really nutritious must plainly be capable for the most part of again serving as nutriment; they are the more worthless in this

respect the higher the degree of oxidation to which they have attained. That is to say, the value of a nutritious substance is chiefly determinable by the amount of potential energy associated with it; *i.e.* by the quantity of kinetic energy or work which may result from its combustion. The more highly oxidized the nutritious substances, the less is the amount of oxygen which they are in a condition to combine with, and the more incapable are they of furnishing energy to the body. Thus urea has no value as a food, creatine very little, while, on the contrary, albumin and sugar are of the highest importance.

The substances which form the essential organic food of the body would be indicated by considering all the regular constituents of the body (pp. 12 *et sq.*), as indispensable to it, and inquiring whether they were capable of formation out of any other substance contained in the animal body; those which were not would of necessity have to be taken into the organism along with the food.

It must, however, here be remembered that in the first place all the substances occurring in the body cannot be regarded as indispensable to it. There is a danger therefore in following the method just given of considering too many nutritious substances as necessary; and a reservation would have to be made on this account. Moreover it must not be forgotten that a certain number of the constituents of the body cannot be replaced by the introduction of a fresh supply along with the food, either because they are incapable of absorption and indigestible (*e.g.* mucin, keratin, cholic acid); or because they unavoidably decompose before they are ingested (*e.g.* muscle-substance in the act of rigor), or are decomposed in the alimentary canal (*e.g.* hæmoglobin by the acid of the gastric juice); or because they would become rapidly changed—oxidized—after absorption, before they could reach their proper situation. Such substances, therefore, are only produced within the organism.

Our efforts to discover, by the above method, the essential constituents of food are chiefly frustrated by our ignorance of the synthetic powers of the organism. In the preceding chapter it was said that, most probably, in the course of assimilation, albuminous bodies were formed from peptones, fats from soaps (and glycerin), and glycogen from sugar. It is, however, yet unknown whether, for example, the results of the further de-

composition of albuminous bodies (leucine, tyrosine, &c.), are capable of synthetic regeneration into albumin. If the organism possessed in general the power of uniting substances synthetically, with the elimination of water, we might briefly indicate the following as necessary organic nutritious substances : viz., the products of the hydrolytic decomposition of all the essential constituents of the body, *i.e.* of the albuminous bodies and their compounds, of the glucosides, of the lecithin-bodies, of fats, &c. These decomposition-products might be contained in food either in an isolated form or already combined into some group, which would in that case be again split up in the course of digestion. The above-mentioned bodies, which have been taken as examples, might therefore be represented in the food in the following ways : (*a*) fatty acids (soaps), glycerin, phosphoric acid, sugar (starch), peptones ; (*b*) fats, phosphoric acid, sugar (starch), albumin; (*c*) lecithin, sugar (starch), albumin ; or (*d*) protagon, albumin, &c.

The question is still further complicated by the circumstance that we do not know whether, in addition to hydrolytic decompositions, other profounder chemical changes (apart from oxidations) do not take place in the body. Fats especially seem to be capable of originating from other bodies than fats and lecithin, for the animal body may contain a large quantity of fat even when the food contains none. Fats might be derived in the organism from the following sources besides those already mentioned :

1. From albuminous bodies, as is indicated (*a*) by the appearance of a fatty body (adipocere) in the albuminous tissues of dead bodies ; (*b*) by the formation of fat out of caseïn in standing milk ; (*c*) by a similar process in the ' ripening ' of cheese ; (*d*) by the appearance of stearin in the body, when, in addition to albumin, a kind of fat (palm oil) containing no stearin is taken with the food (Subbotin). Other phenomena which are cited to prove the formation of fat from albuminous bodies, etc., *e.g.* the ' fatty degeneration ' of organs rich in nitrogen, cannot be regarded as giving any support to the theory, as they simply show that at one part of the organism, which is in connection with every other part by the continual interchange of material, one body is deposited instead of another, and this cannot, of course, be taken to prove that the one is

derived from the other. In like manner, some time since, it was customary to mention among the proofs of the formation of fat from albuminous bodies the fact that the crystalline lens and other nitrogenous bodies destitute of fat when placed in the abdominal cavity of a living mammal became after some time very fatty having lost some of their nitrogen. But all the experiments devised to control this result, in which indifferent porous materials, such as wood, elder-pith, &c., were substituted for the fatless nitrogenous body, have shown that these bodies also become impregnated with fat.

2. From carbo-hydrates. Although the transformation of carbo-hydrates into fats would have to be regarded as a process of reduction—unless indeed we suppose the former to yield only the glycerin necessary for the latter—the following circumstances seem to indicate some such operation : (*a*) Bees fed on sugar alone yield a fatty body, *wax* ; (*b*) Food containing a large quantity of carbo-hydrates tends to fatten the body ('Fattening,' see below), an accumulation of fat taking place immediately, in such cases, in the liver (Tscherinoff). The last-mentioned circumstances admit of another explanation, viz. that the oxidation of the easily combustible carbo-hydrates renders unnecessary the combustion of fat or fat-forming bodies (*e.g.* albuminous bodies); but of this more will be said hereafter. The fact that fats are formed in some fruits (olives) out of carbo-hydrates (mannite) cannot be taken to support the theory that a similar process occurs in animals.

It is now considered that albumin is the only source of the fat in the body, except that which is derived from the fat directly eaten; for in all cases, even in the enormous formation of fat which takes place in milch-cows, the fatty and albuminous materials of the food are sufficient to account for the fat in the milk yielded. Moreover, the production of wax by bees fed entirely on sugar is explicable by the theory of its formation from the albumin stored up; and the fattening of cattle on hydro-carbons is only successful when albuminous food is at the same time taken (Voit).

We are, therefore, guided in the choice of alimentary substances solely by experience, which teaches us that, after water and salts (of which chlorides and phosphates are the chief), albuminous bodies are most indispensable. To what extent true albuminous bodies may be replaced by digestible albuminoids —gelatin and gelatigenous tissues—we shall have occasion to discuss in the third division of the present chapter. It would

seem, moreover, that fats (stearin, palmitin, olein, etc.) may only be omitted from the food when the albuminous bodies are present in it in large excess or when the fats are represented by carbo-hydrates. It is probable, however, that we are not at present acquainted with all the indispensable alimentary substances.

The following are among the more important articles of food :

1. Flesh (muscle) contains, besides water and salts (especially of potassium) amongst the more essential nutritious elements (Chap. VIII.), several albuminous bodies (myosin, albumin), gelatigenous tissues, small quantities of lecithin (possibly derived from the intra-muscular nerves), fats and certain 'extractive matters,' some of which are agreeable to the taste ('osmazome'), while others seem to have weakly stimulating properties (creatine, &c.). It is ingested raw, boiled with water, or roasted. After boiling, the extract—broth of meat—contains chiefly the gelatin, the extractive matters, the salts (which on account of the potassium they contain cause concentrated broths to have an important effect upon the heart, Kemmerich), and some of the fat floating on the surface. The albuminous bodies are insoluble in hot water, and remain behind in meat which is immersed at once into *hot* water; if *cold* water be used, the albumin passes into the water, coagulates as the latter becomes heated, and is removed with the 'scum.' The flesh which remains behind after the removal of the broth still retains most of the nutritious constituents (myosin and the gelatigenous tissues, and albumin if the water used were hot to commence with), but has lost its salts and those bodies which gave it an agreeable flavour. Meat which has been roasted, *i.e.* strongly heated with the addition of little or no fluid substance (water or fat), retains all its constituents; and certain brown, empyreumatic bodies possessed of an agreeable taste and smell are formed in it, especially at the surface.

2. Milk contains albuminous bodies (albumin, casein), fats (butter), and probably lecithin, besides carbo-hydrates (milk-sugar), water, and a considerable quantity of salts. It may be ingested fresh or sour: or the butter alone may be taken ; or the cheese alone. Cheese, however, or the casein precipitated on the acidification of milk, whether occurring spontaneously or on the addition of 'rennet' (the mucous membrane of the calf's true stomach), includes a considerable amount of the fat. On standing, cheese undergoes a change similar to that of digestion, becoming soft and translucent owing to the formation of peptones and the further decomposition of casein. This is called 'ripening,' in the course of which fat is said to be formed out of casein and leucine and tyrosine to appear. Concerning whey and kumiss, see p. 125.

3. Eggs. The white of egg contains a concentrated solution of albumin, while in the yolk are found albuminous bodies, much lecithin, cholesterin and fats, and sugar. On heating, the white coagulates firmly, the yellow into a mass which readily crumbles.

4. Cereals (wheat, rye, maize, barley, rice, oats, &c.) contain an albuminous body (gluten, vegetable fibrin, which are insoluble in water), an albuminoid (vegetable gelatin), lecithin (Hoppe-Seyler), traces of fat, starch in large amount, and, especially at the time of germination, an amyloid ferment (diastase). Grain which has been ground and freed from the husks (bran) is called flour or meal, and is used chiefly in the preparation of bread. On mixing flour with water a tenacious mass, dough, is formed by the action of the latter on the gluten. This dough must be then loosened or rendered spongy, and afterwards heated strongly. The loosening is effected by the evolution in the dough of carbonic acid gas, produced by the conversion of part of its starch, by means of the diastase, into dextrin and sugar, and the fermentation (alcoholic) of the latter on the addition of barm or yeast. The dough thus caused to 'rise' is then heated to about 200° C., which serves to drive off the alcohol at once. The plan of introducing artificially prepared carbonic acid into the dough instead of evolving it by means of fermentation has recently been adopted (aërated bread). Another substance derived from cereals is beer, a watery decoction of grain (malt) which is germinating, and therefore rich in dextrin and sugar. Yeast is added to the decoction, which thereupon undergoes alcoholic fermentation. Beer contains chiefly dextrin, alcohol, bitter substances which are added to it, and absorbed carbonic acid. Of all intoxicating liquors it is the one which contains least alcohol (2–8 p.c.). On distillation, beer and similar fermented liquids prepared from malt (or potatoes) yield a beverage (brandy) very rich in alcohol.

5. Leguminous fruits (peas, beans, lentils, &c.) contain a great quantity of an albuminous body (legumin), besides lecithin and starch. They are eaten for the most part after having been boiled in water, the starch being therefore in the form of a paste. It is not possible to use them in the preparation of bread, as they do not form a dough on account of the absence of gluten.

6. Potatoes chiefly contain starch, in addition to a small quantity of albumin.

7. Fruits which are sweet contain various kinds of sugar, dextrin, vegetable gelatin, very little albumin, and organic acids (tartaric acid, malic acid, citric acid, &c.) Many species, especially grapes, furnish alcoholic beverages—wines—on fermentation of their juices.

8. The green parts of plants (leaves, stalks, &c.), and roots, contain chiefly starch, dextrin, sugar, and albuminous bodies in small amount.

All vegetable alimentary substances contain, as their chief constituent, cellulose, which is almost or entirely incapable of digestion by man and carnivorous animals, but which is probably of great nutritive value to herbivorous animals.

Ingestion of Food.

The ingestion of food takes place voluntarily, at intervals which are, for the most part, of such short duration that digestion and absorption are scarcely interrupted, at least during the

day. It receives its stimulus in certain sensations, hunger and thirst, which have not hitherto been satisfactorily explained, but which indicate the lack of nourishment on the part of the organism. The sense-organs in which this necessity of the whole body makes itself felt as a sensation are certain parts of the alimentary apparatus. Thirst alone takes the form of a localised sensation, a feeling of dryness and burning in the throat, occasioned by deficiency of water in the mucous membrane of the palate and pharynx. This deficiency of water is usually but the local manifestation of the general state of the tissues of the organism. It may, however, be produced by drying the mucous membrane of the throat (by blowing dry air over the part), or by withdrawing the water in some other way (by the application of hygroscopic salts). The feeling of thirst may be allayed as a rule by the local application of water to the parts concerned ; and, as this is accomplished most frequently by drinking, the whole body is at the same time supplied with water. Other methods of introducing water into the system, *e. g.* its injection into veins, also allay it, as would be expected from the circumstance that it results from the general deficiency of water in the tissues (Chap. X., Sec. v.). Hunger, on the contrary, which is a pressing, gnawing sensation in the stomach, and, in its later stages, in the intestine also, cannot be regarded as the local expression of a general lack of nutriment occasioned by deficiency of material in the neighbourhood of the gastric and intestinal membranes. It is, as it seems, a sensation of emptiness in the digestive organs, the conditions of which are yet quite unknown ; for it may be assuaged by filling the stomach, even though it be with indigestible matter. In such a case, of course, a sensation of general lack of nourishment supervenes after a time, which differs from the usual feeling of hunger, but the nature of which is as little understood.

The nerves which minister to the sensation of thirst are probably some or all of those of the palate and pharynx (trigeminal, vagus, and glossopharyngeal). Those concerned in hunger are yet quite unknown. Section of the vagi and of the splanchnics does not diminish the desire for food in animals.

II. EXPENDITURE.

The substances which the body is continually giving up as of no further use to it are :

1. Substances which are quite incapable of taking part in the exchanges of matter, viz. the indigestible portions of food.

2. Those results of the oxidations occurring in the body which are incapable of any further oxidation while within the body, viz. carbonic acid, water, urea, and uric acid.

3. Certain secreted materials which have been poured out on the internal or external surfaces of the body in order to be utilised there, and which, on account of some property, are incapable of reabsorption, *e.g.* the insoluble constituents of bile, the mucus of the alimentary secretions, the fats of the tegumentary secretion, horny substance, &c.

4. A portion of the unoxidizable constituents of the body, —water and salts—which are continually excreted, owing to their physical deportment towards other bodies; for example, water is excreted for the most part as the solvent of other excretory substances.

The above-mentioned substances may be got rid of in the form of gaseous, liquid, or solid excretions. The most important are :

1. The respiratory excretion from the lungs, skin, and intestine (carbonic acid and water).

2. The urine (water, salts, urea, uric acid, &c.).

3. The fluid tegumentary excretions, viz. sweat (water, salts, urea, fatty acids, &c.), and the sebaceous excretion (fats, water, salts, albumin).

4. The fæces (the indigestible portions of food and of the alimentary secretions).

5. The exuviation of epithelium (the shedding of epidermis, hair and nails).

In addition to the above-mentioned excretions, which contain for the most part true excrementitious substances, the body yields up periodically certain of its constituents which are so little oxidized as to be capable of further use in the formation or nourishment of other organisms. They are : 1, Milk; 2, Ova; 3, Semen; which are excretions rich in

albumin, carbo-hydrates, and fat. Menstrual blood may also be included in the list.

Most of the excretions above referred to are direct secretions from the blood, and, as such, have been already described. Thus urine, the sudoriparous and sebaceous excretions, and milk, are treated of in Chapter II., and the respiratory excretion in Chapter IV. Fæces, or the mixture formed in the alimentary canal during digestion, have been mentioned in the description of that process in Chapter III. The remaining excretions, viz. those of epithelium, ova, and semen, consist essentially in the separation of cells or portions of cells. The last two are discussed in the Fourth Section of the book. The exuviation of epithelium takes place in the following manner :— Those internal and external surfaces which are covered with scaly epithelium, viz. the epidermis, the mucous membrane of mouth and pharynx, portions of the urinary and genital organs, and the conjunctiva, lose continually their upper layers of cells after the latter have undergone a peculiar process of shrinking and conversion into a horny material. The horny cells of the external skin, *i.e.* the most external layers of the epidermis, together with the corresponding portion of nails and hair, are simply rubbed off by use ; those of the mucous membranes mingle in the secretions which bathe them (saliva, mucus, urine, tears), and are conveyed out of the body in the fæces or urine as the case may be. This desquamation of epithelial cells is the cause of no inconsiderable loss of nitrogen and sulphur to the body.

III. QUANTITATIVE RELATIONSHIP BETWEEN THE INCOME, EXPENDITURE, AND STOCK OF THE BODY.

At the commencement of this chapter it was stated that the object of the ingestion of food was to repair the losses which the body sustained through the excretion of its inorganic, and the oxidation of its organic, constituents. The simplest relationship which can exist between the food taken and the body is, therefore, when the former is just sufficient to cover the expenditure of the latter, and so to maintain it at its usual standard of weight. In this case it is not, of course, sufficient

that the total gains of the body equal the total losses.   If the chemical composition of the body is to remain unchanged, the amount of the individual chemical constituents of the former must also be equal to the corresponding constituents of the latter.   Moreover, the amount of the food taken into the body and of the individual constituents must constantly adapt itself to the variations in the losses produced by the changes in the extent of the decompositions in the organism dependent on the work done.

The ingestion of food, however, takes place for the most part voluntarily, and is not regulated by any exact knowledge of the needs of the organism.   The sensations of hunger and thirst which give indications of the necessity for food only prompt as a rule to its ingestion, and not to its ingestion in definite quantity; and, indeed, food is very frequently taken without any such prompting.   The ingestion, therefore, of superfluous or insufficient amounts of food occurs very often.   In the former case we may suppose one of the following sets of circumstances to take place: 1. The losses of the body may remain the same while the body-weight increases, the amount of potential energy in the body becoming increased and stored up.   2. The superfluity of nutriment may remain unabsorbed, and pass unchanged out of the body in the fæces.   This only occurs when the superfluity is excessive.   The maximum power of absorption, in the case of the more easily absorbable alimentary substances, is first attained in the case of salts,[1] then in the case of fats, and finally in the case of water.   3. The superabundant alimentary substances may be absorbed and immediately re-secreted without any further change.   This only occurs in the case of water and salts, the excretion of which proceeds until the body possesses its normal quantity (p. 183).   Unoxidized organic bodies are never found under normal circumstances in any excretions except milk, ova, and semen.   4. Such an excess in the amount of the food taken may be followed by increase of the decompositions and oxidations occurring within the body and of the work done, the losses of the

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[1] The absorption of the easily soluble salts, which usually takes place rapidly, is interfered with, when they are ingested in larger quantities, by the circumstance that they render the contents of the intestine fluid by their attraction for water, and so cause their rapid excretion (diarrhœa) before absorption can occur.

organism increasing while the body-weight remains unchanged. 5. It is conceivable that even without any marked increase of the oxidation-processes going on in the body, its weight may be maintained nearly constant, *e.g.* by the decomposition of the constituents of the body, which are in excess of the immediate wants of the organism, into substances rich, and into substances poor in energy, of which the former may be retained in the body, whilst the latter are excreted. In this manner the energy contained in the *ingesta* would, as it were, be concentrated, *i.e.* associated with a lesser weight of matter, so that there might be an increase in the stock of potential energy at the disposal of the body, unaccompanied by any appreciable increase of its weight.

In the contrary case, when an insufficient amount of food is ingested, one of the following results may occur: 1. The work done by the body and the various losses to which it is subject may remain as before while its weight decreases. 2. The body-weight may be unaltered while the expenditure or losses of the body diminish. As, however, the second of these possibilities is limited by the circumstance that a certain amount of work, accompanied by the using up and loss of a certain amount of material, is indispensably necessary to the maintenance of the body, the diminution in the amount of food taken must sooner or later reach a point after which the weight of the body must decrease until life is no longer possible.

To test experimentally the accuracy of the theories here laid down is the aim of the department of physiology now being considered. By a long series of experiments on man and the lower animals, in which the conditions of excess, sufficiency, or insufficiency of food were artificially arranged, and the amounts of the gains and losses of the body individually and collectively estimated, it has been sought to discover (1) which elements of the body are excreted under normal circumstances, when no increase by special activity occurs in the materials used up; and hence the quantity and composition of the food necessary to repair the losses thus sustained; (2) how the material exchange varies when repair is insufficient; and (3) how it varies when an excess of alimentary substances is administered. The results of these experiments will now be given in order.

1. *The necessary Losses of the Body and their Reparation by means of Food.*

In order to decide what losses sustained by the body are indispensable, and what amount of food is therefore necessary for their repair, two methods are possible, neither of which leads, however, to absolutely correct results. The first consists in giving a man or an animal the smallest amount of food requisite for the maintenance of the weight of the body, and in analysing the excreted substances under these conditions, the elements of which should correspond quantitatively with those of the food : the second, in depriving an animal of all food, in which case we may be certain that no material is unnecessarily excreted, and then determining the necessary elements of food by analysis of the excreta.

The first method possesses the following sources of error : 1. The process itself is a working in the dark, and leads with difficulty to an exact result. 2. The difficulty of excluding all unnecessary use of material such as would be occasioned by movements, &c. 3. The uncertainty whether the amount of food which is just sufficient to maintain the weight of the body at its normal, would not be found to be less if its composition were more judiciously arranged ; or, in other words, whether certain of the constituents of the excreta are not due to an excess of the materials ingested. 4. The difficulty in estimating the elements of the fæces. The fæces contain (Chap. III.) not only the results of material exchanges (portions of the alimentary secretions), but also the indigestible parts of food, which must by no means be reckoned among the losses of the body due to the repair of its tissues, but are to be attributed to the accidental composition of the food itself. The fæces of herbivorous animals, for example, form almost the half of the total excretions of the body (in horses 40 to 50 per cent., Valentin, Boussingault ; in cows, 34·4 per cent., Boussingault) on account of the considerable quantity of indigestible material contained in vegetable food. In carnivorous animals, on the contrary, the proportion is very unimportant (in cats 1 per cent., Bidder and Schmidt). In omnivores it is intermediate (being in men 4 to 8 per cent., Valentin, Barral, Hildesheim ; and in pigs 19·9 per cent. Boussingault), and varies from time to time with the kind of food. In order to eliminate this very varying and unnecessary factor in the calculation of the losses of the body, we must either disregard the fæces altogether—in doing which another error is introduced by overlooking the real elements of loss which they may happen to contain—or we must choose alimentary substances which contain no indigestible portions —an experiment which has not yet been tried.

In the second method a great error is introduced by the circumstance that in famished animals the various functions quickly become languid, and,

in consequence, the use of material and the losses of the body less than when a sufficiency of food is taken.

Of the results yielded by the above methods of experiment, those relating to the relative quantities of the excreta are the most certain and important, as they teach at the same time by what channels the various elements of the body are separated.

1. The total losses of the body, after subtracting the fæces which are most variable in quantity, are referable in about an equal extent to the urine on the one hand, and to the sudori-parous and respiratory secretions on the other. In this division the following are neglected: the true elements of loss contained in the fæces (constituents of bile, &c.), the sebaceous secretion, and the exuviated epithelial cells, concerning which no determinations have as yet been made. In carnivorous animals the urinary secretion is for the most part somewhat in excess of all the others, including the fæces. In herbivorous animals, on the contrary, it only amounts to one-eighth or one-third of the other secretions. The cause of this lies chiefly in the greater amount of fæces excreted by the latter.

2. The elements which compose the inorganic constituents of the body (water and salts), and which are excreted and res-tored in similar combinations, are the following:

a. Water. The proportionate amounts of water separated by the various excretions, if we except that separated in the fæces, which is generally of small amount, depend chiefly upon the temperature and the hygrometric state of the atmosphere. The loss of water from the lungs is almost constant, as there the same extent of surface moistened to the same degree constantly comes into contact with the atmosphere by means of a stratum of air which is continually in motion. Moreover, the loss of water by cutaneous respiration cannot be distinguished from that which occurs in the secretion of sweat; hence, both may be taken together. Therefore, it may be said that the chief loss of water is referable to the lungs, skin, and kidneys. For reasons which are very apparent, it will be seen that with a dry, warm atmosphere, the loss of water from the skin will be greater than that from the kidneys, while with a moist, cold atmosphere, the reverse will obtain. That the total amount of the excreted water depends upon the amount ingested has

already (p. 115) been indicated; and more will be said below in reference to this matter in speaking of the ingestion of excessive amounts of food. In carnivores almost the whole of the water (as much as 90 per cent.) is got rid of from the kidneys; while in herbivores as much as 60 per cent. passes away in the fæces.

b. Salts are chiefly excreted in the urine; some, however, appear in the sweat, while a few (mostly those of potassium and the indigestible salts) pass out of the body in the fæces, together with any superfluity of salts which may have been ingested.

3. The elements of the (oxidized) organic compounds of the body are excreted for the most part in the form of inorganic products of oxidation, and less frequently as organic products of oxidation or decomposition. They are:

a. Carbon, by far the largest portion (more than 90 per cent.) being excreted in the form of carbonic acid in the process of respiration. A smaller amount is separated in the form of less highly oxidized products during the other processes of secretion (in urea, uric acid, &c.; in the horny substance of epithelium, the sebaceous secretion, the constituents of the secretions contained in the fæces, &c.).

b. Hydrogen (*i.e.* that derived from the organic constituents of the body) is separated for the most part in the form of water, together with the water which previously existed as such in the body. A small portion quits the organism in the organic compounds mentioned under *a.*

c. Oxygen (*i.e.* that derived from the organic compounds of the body) is excreted together with that taken into the system for the purposes of oxidation, the amount of the latter kind being from three to ten times as great as that of the former. By far the greater proportion is separated in the highest forms of oxidation, viz. as carbonic acid and water, only a small amount being excreted in the lower forms as urea, &c.

d. Nitrogen is excreted entirely in the form of decomposition-products, for the most part as urea in urine and sweat, but also as uric acid, urinary colouring matter, horny substance, biliary constituents, and possibly in small amounts, as ammonia and pure nitrogen.

The old question whether, when the body-weight remains the same, all the nitrogen taken into the system reappears in the visible excretions (especially in urine and fæces), or whether a part only is so excreted—a circumstance which would compel the admission of a separation of nitrogen in the lungs—seems now to have been settled in favour of the former alternative (Voit, Siewert, Schulze and Märcker [Henneberg], Stohmann : this view is, however, opposed by Seegen). In the special case where the food happens to be very albuminous, it is still maintained by Stohmann that the amount of nitrogen recoverable from the visible excretions is less than that ingested. When cutaneous perspiration takes place such a comparative deficiency of nitrogen is observable owing to the excretion of that body in the sweat (Leube).

e. Sulphur (derived especially from the alkaline albuminates of the body) leaves the organism, about half of it in the form of sulphates in the urine, and the rest, combined in various organic compounds, in epithelial exuviations and in the fæces (keratin, taurine).

The data for the determination of the absolute amount of the minimum excretion of the body, and of the minimum quantity of food necessary to repair the losses occasioned by that excretion, are still less definite, more especially because of the uncertainty before mentioned attaching to the methods of investigation (p. 202). The following is an epitome of the results which have been obtained :

• 1. The minimum excretion (or ingestion) is larger the smaller the animal observed. For the purposes of comparison, the material exchange, in twenty-four hours, per kilogramme of the weight of the animal, is determined. It is thus found that in pigeons a far larger exchange of material occurs for every kilogramme than in dogs ; while in the latter it is far greater than in man. This is explained by the greater activity of the vital processes in smaller organisms : small animals, for example, on account of the comparatively larger extent of surface which they expose, must generate more heat than large ones, in order to maintain their temperature (Chapter VII.).

2. The minimum amount of food necessary is lowest when the elements of the food are mingled together in a definite manner. Such a perfect mixture of the elements of food contains proteids, fats or carbo-hydrates, possibly also lecithin, water and salts in certain proportions, the salts being present in smallest amount, and water in greatest.

3. The most favourable relationship of these elements one to

another, *i.e.* the proportion that must exist among them so that the smallest amounts may be able to maintain the normal weight of the body, varies in the varying conditions of age, sex, and mode of life.

4. Up to a certain point the amount of albumin usually considered necessary in the food may be decidedly diminished by increasing the amount of fats or carbo-hydrates : possibly, as Hoppe and Voit suggest, because every body which oxidizes more easily than albumin prevents the action of oxygen on that body by attracting it to itself.

5. The minimum amount of food necessary is greater according as the organism is already fattened by excessive feeding.

The absolute numbers obtained by the methods before mentioned are, on account of the sources of error to which those methods are open, only of value when all the experimental conditions are exactly carried out. They will therefore not be given here. It should also be mentioned that circumstances, such, for instance, as temperature, have an influence upon the utilization of material in the body.

2. *Insufficient Ingestion of Food.*

It has already been said (p. 201) that if the food administered be insufficient in amount, a time must of necessity come after which the body-weight will steadily decrease. In the case of starvation, when there is a complete deprivation of food, this diminution in body-weight commences at once ; and sooner or later, according to the condition of the animal at the commencement, a period arrives at which the functions of the body, as well as its losses, begin to diminish ; this diminution continues until death. The material exchanges which occur in fasting animals merely consist in the combustion of the constituents of the body by means of the oxygen continually inspired, and the excretion of the products of that combustion, and of the incombustible constituents, water and salts. The organism, as a whole, undergoes in the meantime no repair ; but, in all probability, certain portions of it are restored at the expense of others by the action of the blood, which transfers to the former the energy-yielding materials which the latter may contain in superabundance.

Observations of the material exchanges of fasting animals (Experiments on Inanition) extending over considerable periods have only been made on

the lower animals, chiefly on pigeons (Chossat), dogs (Bischoff and Voit), and cats (Bidder and Schmidt).

The following generalisations have been made from experiments on fasting animals:

1. At the beginning of the process of starvation the body-weight, the activities and the losses of the body all decrease. The diminution in the losses of the body naturally causes the decrease in its weight to become less from day to day ; for the sum of the losses or excretions, after subtracting the amount of the oxygen taken into the body, expresses directly the loss of the body in weight (see Fig. 4). The diminution in the bodily energies or activities, which is intimately connected with the decrease in the losses, is indicated especially by a low temperature and an infrequent pulse and respiration, the diminished income of oxygen thus brought about occasioning a diminution in the processes of oxidation.

2. The diminution in the excreta does not affect all their elements equally. Herbivores exhibit the most considerable alteration in the composition of their excreta ; for all fasting animals may be regarded as carnivores, since they subsist on nothing but the constituents of their own bodies. Thus, in the case of fasting herbivores, the amount of urea in the excretions at first increases (p. 111). As a rule, however, the amount of urea in the excretions diminishes as the time during which no food has been taken extends—a proof that the decrease in the processes of oxidation in the organism concerns also the oxidation of the nitrogenous (albuminous) constituents of the body. The diminution in the amount of urea excreted is at first abrupt, and the more so the larger the amounts which were normally excreted before starvation commenced ; later on, the excretion of urea diminishes slowly and regularly. While, therefore, in the later periods of starvation, a certain proportion of the albumin of the body (organic albumin) is regularly used up, at the commencement it is the stored-up albumin derived from the food last ingested which is expended (Voit).

3. After the animal has lost a certain fraction of its weight, death by starvation supervenes, the interval preceding it from the commencement of starvation varying in different individuals. The length of the interval, and the amount of the loss which the animal is able to sustain before death, depend upon the

condition of the animal previously. Animals which have been fattened require a certain time longer to allow of their weight attaining its normal condition; for not until this has been accomplished does any diminution in the losses and activities of the body occur, and starvation, therefore, really commence. Thus, young and poorly-fed pigeons die in three days after losing one-fourth of their weight, while old and well-fed birds will live for thirteen days, until they have lost nearly the half of their former weight (Chossat).

4. The amount of loss in weight differs much in various parts of the body. The oleaginous contents of the fatty tissues (or, briefly, the fat) diminish most, the whole tissue losing from 91 to 93 per cent., *i.e.* the connective-tissue alone remains. The abdominal viscera and muscles lose less weight than the fat. The brain and spinal cord lose extremely little; the former, however, somewhat less than the latter. The blood, it may be noted, especially in the amount of its hæmoglobin, maintains approximately its relationship to the whole weight of the body. This inequality of loss in the various parts of the body is brought about by the power before referred to which the blood has of conveying material from one organ to another, and thus securing as perfectly as possible the nourishment of the organs most frequently used. This is indicated not only by the fact of the slight loss of weight of the brain, the activity of which continues undiminished until death, but also by the smallness of the loss sustained by those muscles which are continually in use, as compared with the loss sustained by those which are less active. As fat and muscle are the chief elements in the losses of animals when fasting, it is generally stated that animals in such a condition live upon their own fatty and muscular tissues. Certain investigators (Schmidt, Bischoff and Voit) have even calculated from the nitrogenous elements of the excreta the quantity of such muscular substance used, and have considered all the remaining elements which are referable to the organic constituents of the body (calculated from the carbonic acid excreted) as effete fatty material.

In addition to the case of total deprivation of food, we must consider that in which food is administered in insufficient quantity. This insufficiency may be quantitative or qualitative, *i.e.* the food taken may contain all the necessary elements

of food, but in insufficient quantities, or it may not contain all the essential elements. Quantitative insufficiency induces all the symptoms of complete starvation, but much more slowly. Qualitative insufficiency in most cases terminates in death as quickly as complete starvation, but with a less diminution in the body-weight. During complete deprivation of water [1] (Schuchardt) animals very quickly cease to take solid food; and, on the contrary, during complete deprivation of the solid constituents of food (Bischoff and Voit, Chossat), they very soon refuse to take water: each, therefore, may lead to starvation. In most combinations of the alimentary elements in food, the observations are interfered with, either by the fact that the maximum absorption becomes so slight that it is impossible to study the effects of large amounts, or by the appearance of morbid symptoms, *e.g.* of diarrhœa when the combination consists of sugar and water. Those experiments are of most importance in which one of the two chief organic alimentary substances, albuminous bodies or fats (carbohydrates), is withheld from an animal. In such cases the general loss to the body is considerably less than in fasting animals; each of these elements of food, therefore, can replace the other to some extent. On withholding the albuminous elements (as by feeding on fat and water, or on fat, carbohydrates and water) the excretion of urea becomes considerably decreased, while the weight of the body undergoes a certain but not excessive diminution, indicating that the oxidation of nitrogenous bodies is proceeding less rapidly than usual within the organism. On withholding fats, no marked alteration in the material exchanges of the body occurs if the food contain instead carbo-hydrates. If the latter are also withheld, a very decided increase occurs in the excretion of urea, indicating an increased oxidation of nitrogenous materials, and necessitating an increased ingestion of nitrogenous food in order that life may be maintained. No essential disturbance in the body is occasioned on the removal of sodium chloride from the food; and on deprivation of phosphoric acid the bones retain for a long time the phosphates they happen to possess (Weiske).

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[1] That is to say, of that also which is contained in the organic alimentary substances; for many animals (*e.g.* cats, Bidder and Schmidt) can do very well without actually *drinking* water.

Albumin may for certain purposes be replaced by gelatin; for the addition of gelatin renders unnecessary the use of so much albumin as before, as is proved by the body-weight maintaining its normal standard under such circumstances. As, however, the weight of the body rapidly falls when gelatin is the only nitrogenous element in the food, it is evident that the necessity of the tissues for albumin cannot be met entirely by that substance (Voit).

3. *Superabundant Ingestion of Food.*

As has already been mentioned, the income of the body is very often greater than is necessary to cover the (minimum) expenditure, and to maintain the body-weight at its normal weight; and this excess may affect some or all of the essential elements of the food. We have now to determine which of the possible, methods mentioned on pp. 199 *et sqq.* is adopted for the disposal of the excess. The question is simplified by excluding: (1) All excess of alimentary substance taken into the body over the amount which is capable of absorption (as determined by the maximum absorptive power of the body for the particular substance, p. 200). (2) All increased ingestion of food rendered necessary by the increased activities of the body (formation of heat, mechanical work—see the second Section of this book). Moreover, any excess of inorganic elements of food—water and salts—may be left out of the question; for, as already mentioned, the body gets rid of any superfluity of those bodies by direct excretion from the blood—the water through the skin and kidneys and the salts through the kidneys.

There remains, therefore, the case where an excess of organic alimentary substances has been ingested. For its disposal three courses are possible: 1. It may be simply retained in the organism. 2. It may be quickly oxidized and excreted. 3. It may be decomposed, and a part oxidized and excreted, while the rest, which is capable of yielding energy, is retained (p. 201). In the first case, the weight of the body would increase while the losses remained constant; in the second, the losses would increase while the body-weight was unchanged; and in the third both would increase. Experience has shown that if an excess of food be ingested, the body increases in weight; that the excretion of the products of oxidation is also increased, especially (C. G. Lehmann, Bidder and Schmidt) in the case

of urea, when the excess consists of nitrogenous food; and, finally, that the materials never make their appearance in the excreta in an unoxidized form. The first of the above-mentioned courses is, therefore, excluded by the circumstance that the excretions always increase. The second, besides that it does not tally with the experimental fact of an increase of weight in over-fed animals, would necessitate a corresponding increase in the amount of oxygen taken into the body, and in the bodily energies or activities, in consequence of the increased extent of oxidation. In a reposing body this increase in the bodily energies could only manifest itself by an increased formation of heat (Chapter VII.). Such an increased formation of heat does, in fact, occur; the augmented digestive activity requiring a greater consumption of material and yielding more heat in the processes of secretion and movement; but the amount is too slight to satisfy the second theory. The following facts support the third of the above methods of disposal.

As in the case of an insufficient allowance of food, so here also where the food is administered in excess, the expenditure of the body accommodates itself to a certain extent to the income. This accommodation has been most exactly made out in the case of the albuminous elements (Bischoff, Voit). Whenever an animal is fed for a long time abundantly with albumin, a condition of equilibrium supervenes, after a short time, between the nitrogen in the food and that in the excreta; and this equilibrium is connected with a definite weight of body, which is meanwhile maintained. If the amount of food is suddenly increased, and maintained at the increased rate, the equilibrium is again established, after a certain time, with an increased body-weight. Until this state of equilibrium is reached the excreta are somewhat less than the ingesta, and albumin is stored up in the body, the animal being said 'to make flesh.' If, on the contrary, the amount of albuminous food is diminished, the excreta continue to be somewhat greater than the ingesta in the interval preceding the readjustment of equilibrium with a diminished body-weight; and the animal 'loses flesh.' The organism can, therefore, within certain limits, 'readjust itself,' for every alteration in the amount of the food ingested, its constitution undergoing a change in the

process. If the amount of food ingested is diminished below a certain point, the condition of hunger supervenes, the laws of which are similar to those above given.

The following figure serves to illustrate diagrammatically what has been said. The abscissa-line AA′ indicates the time, the ordinates of the thick curve the weight of the body, or its albuminous constituents, those of the thin curve the amount of the daily excreta, and those of the dotted one the amount of the daily ingesta. The ingesta are suddenly increased in amount at *a*, and at *c* suddenly diminished, and are at *e* nothing. A*a*, *bc*, *de*, indicate the periods of states of equilibrium between ingesta and excreta; *ab*, the period during which readjustment is in progress when the excreta and the body-weight are both increasing; *cd*, the period during which readjustment is taking place when the excreta and the body-weight are both diminishing; *e*A′ the period of hunger, also characterized by the decrease of both body-weight and excreta. The alterations in the weight of the body on each day are of course determined by the difference between ingesta and excreta.

FIG. 4.
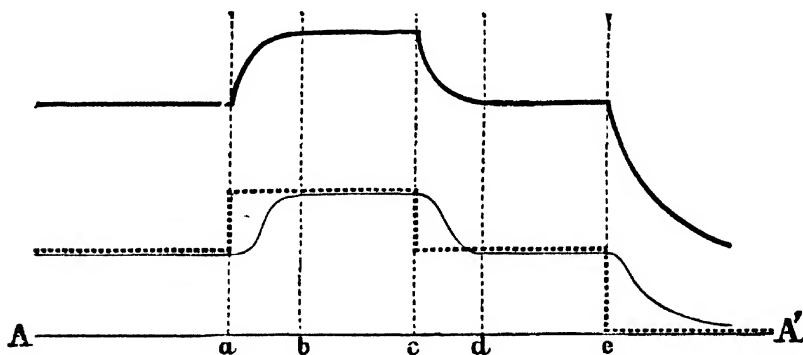
According to recent investigations (Pettenkofer and Voit), it would seem that a similar relationship between income, expenditure, and stock exists in the case of fat as in the case of albumin. The amount of fat stored up in the body is, however, also dependent upon the albuminous ingesta. When, therefore, the latter are increased in amount, there occurs not only an accumulation of albumin, but also of fat. Fat is probably formed (p. 194) during the decomposition of albumin under certain circumstances;—a decomposition, attended with excretion of urea and retention in the body of certain energy-yielding complex molecules, such as is contemplated in the third of the three possible courses mentioned above. What the circumstances are which are favourable to this formation of fat, and whether they are connected with the excessive

ingestion of food, cannot yet be exactly stated. On the other hand, the expenditure of albumin is diminished by the simultaneous ingestion of fats or carbo-hydrates, of which fact no explanation has hitherto been given. The very general statement that fats and carbo-hydrates, being easily combustible substances, attract to themselves the oxygen, and in that manner save the albumin, is not very well founded. That the addition of a fatty element to an albuminous diet leads to the accumulation of fat in the body is most probably to be explained by the direct accumulation of the fat ingested, or the diminished use of that already present. The statement that carbo-hydrates have the same effect as fat in this case is disputed; it certainly remains at present quite unexplained.

The increased expenditure of albumin when it is ingested in greater quantity is connected with an increase in the amount of oxygen used (Pettenkofer and Voit); and the decompositions which take place are, therefore, concluded to be oxidations. In the attempt to calculate the amount of albumin consumed from the nitrogen eliminated, it is found that only a portion of the carbon is present in the excretions—a proof that, in the decomposition, some constituent rich in carbon is retained in the body (Pettenkofer and Voit). The seat of these processes is entirely unknown. It used formerly to be stated that the superabundance of ingested albumin was simply burnt up in the blood without first forming part of any organ (' Luxus-consumption'). It is, however, now considered much more probable, especially as no one has ever succeeded in demonstrating the existence of true processes of oxidation in the blood, that all decompositions are accomplished in the cells of the organs, and are only influenced in some unknown manner by the extent to which blood is present. The formation of fat is always brought about by means of cells, as may be demonstrated. Adipose tissues, especially of the mesentery, are to be regarded according to modern research (Toldt, Rollett), not as simple connective-tissue, the cells of which are filled with fat (Virchow), but as glandular organs with special vessels, which in man are early surrounded by a growth of connective-tissue.

The decomposition of a portion of the albumin in the intestines into leucine, tyrosine, &c. (p. 107) has recently been regarded as a case of ' luxus-

consumption.' Many observers consider even peptones as albumin set apart for direct combustion (p. 185).

The consumption of albumin, besides being dependent on the addition of albumin, fats and carbo-hydrates present in food, is determined to a certain extent by the salts ingested. A moderate ingestion of sodium chloride especially is said to diminish the expenditure of albumin (Klein and Verson), while an excess increases it (Voit). The addition of water also has an influence; free ingestion of water increases the excretion of urea, which must be attributed to an influence upon the decomposition of albumin, as mere physical conditions cannot effect any increase in the amount of the urea. Increase in temperature causes an increased consumption of albumin. For the influence of muscular activity see the following Section of the book.

The reason why food is generally ingested in superabundance is because the weight (and dimensions) of the organism increase continually from birth to maturity, this increase being called growth; and also because, thereafter, certain regular excretions of unoxidized materials occur both in males and in females, viz. in the former semen, and in the latter menstrual blood and the excretions destined for the use of the developing ovum, and at a subsequent period milk for the nourishment, of the child. This matter is treated in Section IV. of the book.

PART II.

THE ACTIVITIES OR ENERGIES OF THE BODY.

INTRODUCTION.

In the general Introduction to this work it is stated that the animal body is the seat of transformations of potential into kinetic energy.

It may be stated generally that the potential energy of the body is associated with two kinds of matter, widely separated from one another, viz. atmospheric oxygen on the one hand, and the oxidizable constituents of the body, which enter it as food, on the other. Energy-yielding substances are, therefore, being continuously introduced into the body. It has, further, already been stated, that the products of the combination of the above-mentioned different kinds of matter, *i.e.* oxidation-products, are continually being thrown out of the body.

Similarly, it has now to be stated that the energy which has become kinetic in the animal body is continually being transferred from it to bodies existing in the medium outside and independent of it. Just as, however, the expenditure of the matter of the body is always a little below its income (and this difference is necessary to the existence and persistence of the body), so also the expenditure of energy is always below its income, for the organism always contains a certain store of energy, part of which is potential in its yet unoxidized constituents, part of which is kinetic—its heat.

The transformations of the energy of the body run side by side with the exchanges of its matter. As in the preceding chapter, the income and expenditure of the matter of the body have been discussed and compared, the same task must now be

undertaken in reference to its energies, whilst these must, as far as possible, be brought into relation with the exchanges of matter. The scanty knowledge yet possessed on this subject merely permits of the discussion of some of its salient points.

Introduction of Potential Energy into the Body.

Although the potential energy which has here to be considered is associated, not only with the matters to be oxidized, but also with oxygen, we usually only speak of the energy of the alimentary substances of the food, whilst we tacitly and correctly assume the presence of the quantity of oxygen required to oxidize them. The potential energy of the oxidizable (organic) alimentary constituents is usually expressed as heat, *i.e.* the total kinetic energy which can be developed by the oxidation is represented as heat, although, as can be proved, forms of energy other than heat arise from them.

This simplification possesses great advantages for quantitative determinations.

The determination of the heats of combustion of the alimentary substances is easily effected by burning them in a calorimeter, *i.e.* a chamber surrounded on all sides by some liquid, generally water. The temperature of the liquid, the amount of which is known, is determined before and after the combustion. The result, which is the amount of heat produced, is expressed in 'units of heat' (see page 5), and furnishes a measure of the heat of combustion. The difficulties which attend this experimental determination are, however, great in the case of many of the alimentary substances, so that the heat of combustion of many is not accurately known.

Although, in the animal body, the combustion of the alimentary substances (or of the constituents of the body which originate from them) does not take place suddenly, as is the case in artificial combustion, but gradually, yet the results of calorimetrical determinations do afford a measure of the heat developed in the slower oxidations; for *the sum of all the heats developed in the individual successive oxidations, or decompositions of any other kind, which a body undergoes before it is completely burned* (so as to yield carbonic acid, water, sulphuric acid, &c.) *is equal to the heat which is directly developed by perfect combustion.*

A method of very simply determining the heats of combustion which has been adopted by some scientific men is not trustworthy, and leads to false results. They have, namely, attempted to calculate the heat of combustion of a compound from the known heats of combustion of its elements; to do this they suppose the oxygen which exists in the compound itself to be already combined, partly with hydrogen or carbon; it appears, however, firstly, that the basis for such a hypothesis is wanting; and secondly, that the other elements of a compound are bound together with a certain amount of energy, so that to separate them one from the other, a portion of the kinetic energy developed in the combustion must be consumed: the results obtained by such a method must therefore differ from the results of direct experiment by an amount which corresponds to the energy used up in the dissociation process just referred to.

In the case of chemical compounds of *known constitution* (and few of the alimentary substances can as yet be classed under this category) the heats of combustion can be calculated according to simple rules (Hermann).

From experimental determinations it has been made out that in complete combustion 1 gramme of albumin generates 4998 heat units, 1 gramme of beef (freed from fat) 5103 heat units, 1 gramme of beef fat 9069 heat units. When oxidized so as to yield urea, albumin is calculated to furnish 4263, and beef 4368 units of heat (Frankland). By calculation it is found that 1 gramme of stearin develops 9036, 1 gramme of palmatin 8883, 1 gramme of olein 8958, 1 gramme of glycerin 4179, 1 gramme of leucine 6141, and 1 gramme of creatine 4118 units of heat (Hermann).

Origin of the Kinetic Energy of the Body.

(*The Energies of the Body.*)

Oxidation (as has already been repeatedly stated) is the process which, far more frequently than all others, leads to the transformation of potential into kinetic energy. We cannot, nevertheless, forget that oxidation is not the only process associated with the liberation of energy, but that it is only one of the processes, though certainly by far the most frequent, which prove the general law that *in every chemical process, in which stronger affinities are saturated than were saturated before its occurrence, potential energy becomes kinetic.*

An example of a process not dependent upon oxidation in which, however, heat is generated is afforded by the alcoholic fermentation of sugar.
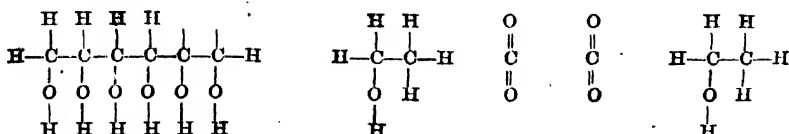
$$C_6H_{12}O_6 \text{ splits up into } C_2H_6O + CO_2 + CO_2 + C_2H_6O$$

As the above graphic formulæ indicate, carbon atoms, which in sugar are linked either to carbon or hydrogen atoms, are, after the decomposition, linked to oxygen atoms. As, however, the attraction of carbon for oxygen is greater than it is for carbon or for hydrogen, this change in the position of atoms must be associated with the liberation of energy. As these groups of atoms which result from such a process of decomposition are bound together by stronger affinities than those which existed before, the new compounds are more stable; and it may be stated as a general proposition that in operations attended by the formation of chemical compounds, or of more stable compounds than existed before, potential energy becomes kinetic. Under this general law are included the ordinary processes of oxidation, as well as others which are analogous to the fermentation of sugar.

The forms of energy in which the kinetic energy developed in the body from the potential energy introduced into it may manifest itself are, so far as we know, heat, electricity, and mechanical work. When the animal body is in a state of rest, viz. when all kinds of work which are not absolutely essential to the continuance of life are avoided, it may be stated that all these forms of energy are almost entirely transformed into a single form—heat.

The form which energy (see the Introduction) may assume is, as we know, very variable; heat is easily converted into motion (as in the steam-engine), motion into heat (by friction); both heat and motion into electricity (frictional- and thermo-electricity); and electricity into heat (as evidenced in the heating of wires along which a current of electricity is passing) and into motion (electro-magnetism).

Nevertheless the amount of kinetic energy always remains constant, though such transformations occur, for they always proceed in definite proportions (equivalents). The most important of these equivalents is the 'Mechanical Equivalent of Heat,' *i.e.* the mechanical work into which a certain amount of heat may be converted, or conversely.

The *formation of heat* goes on directly in all organs of the body in which processes of oxidation occur, *i.e.* in all, except the horny, tissues.

Electricity, so far as we yet know, is only developed in the muscular and nervous systems (Chapters VIII. and IX.).

Movements occur with perceptible rapidity, 1. in the striped and smooth muscular fibres; 2. in contractile cells; 3. in ciliated cells; 4. in spermatozoids; whilst other movements take place with such slowness in all organic forms that they cannot be perceived; such occur during growth, in the fission of cells, &c.

The proof that, in the body when in a state of rest, all forms of energy are converted into heat, and are in this form transferred from it to the external world, rests upon the following facts:

1. Movements which occur in the body when at rest do not, as such, exert any action upon the medium outside of it, but disappear within the body itself. This disappearance is brought about chiefly by *friction*: thus, the whole of the kinetic energy of a cardiac contraction expended on the mass of the blood imparts to it *motion*; in the course of the circulation this motion, by friction against the walls of the blood-vessels, and especially of the capillaries, ceases to exist. This same disappearance of motion is observed in the case of the alimentary apparatus, where it occurs partly in consequence of friction against the contents and against the structures which surround it.

As no other mode of motion (*e.g.* electricity) is known to result from this friction, we are led to suppose that, everywhere, a quantity of heat is generated which is equivalent to the motion, *i.e.* mechanical work, which disappears.

2. Even the small quantities of electricity developed in the nervous and muscular systems appear, in great part, to be converted into heat (Chapter VIII.).

Exceptions which, judged of quantitatively, are of very small importance must be made to the general statement previously enunciated, that in the body at rest, the only form of kinetic energy imparted to the medium around it is heat: thus, (1) the movements of respiration, of the heart, of the pulse may be communicated to bodies outside the organism; and (2) electric currents may be conducted away from the surface of the body to surrounding objects by the interposition of conducting media (Chapter VIII.).

In the animal body when at work there originates an increased quantity of kinetic energy, in addition to that which is being produced during rest. This energy, which is developed within the muscles, takes the form of heat and mechanical work. Of this mechanical work a great part is converted, within the organism itself, into heat by the friction of the muscles and tendons within their sheaths, and by the movement of bones in their articulations. The remainder of the mechanical work is employed, partly in effecting the movement of the various parts of the body in reference to one another, partly in moving the body as a whole through the medium

which it inhabits, and partly in effecting the movements of bodies which exist in that medium.

Seeing that even the last-named portion of the energy of the body (viz. that expended on the bodies of the external world) is easily converted into heat, and may be expressed in *units of heat*, it is evident that the natural measure of the whole of the energies of the body is the amount of heat corresponding to them.

One might, naturally, just as well express the whole energy according to its mechanical equivalent, *i.e.* in units of work instead of units of heat (as kilogrammetres, foot-pounds, &c.).

The numbers of heat units which express the kinetic energy of the organism are enormously great, amounting to several millions per diem. Some employ in their calculations an unit of heat which is a thousand times greater than that usually employed, defining the unit of heat to be that quantity of heat which will raise one kilogramme of water from 0° C. to 1° C.; the mechanical equivalent of this unit is then = 424 kilogrammetres.

Expenditure of Energy.

With the exception of the small quantity of energy which the organism loses in its imperfectly oxidized organic excreta (urea, uric acid, milk, &c.), all the potential energy of its food passes as kinetic energy to the outer world. From what has been previously stated, this energy escapes from the body at rest only in the form of heat, whilst in the case of the body which is doing external work in the form of heat and mechanical work. The modes in which heat is given out to the bodies of the outer world will be treated of in the following chapter; the transfer of mechanical work needs no further discussion.

The direct measurement of this expenditure of energy (heat) is effected, in the case of the body at rest, by placing the man or the animal, exactly as a burning body, into a calorimetrical chamber adapted to the purpose. In the case of the body engaged in performing external work an arrangement is provided within the chamber which permits of the work done being measured; such, for example, as a treadmill which is connected with a steam-engine, and which the man under observation ascends or descends, so as to perform an amount of work (either in accelerating or retarding the movement of the wheel) which permits of being estimated (Hirn). From the quantity of mechanical work thus estimated the

equivalent number of units of heat may be calculated and added to the expenditure of heat as found by the direct method.

(For the magnitude of the expenditure of heat and of the mechanical work done as well as for their relations, consult the two following chapters.)

Comparison between the Income and Expenditure of Energy.

The object of attempting a comparison between the energy which enters and leaves the body is, firstly, to confirm the theoretical conceptions which we have formed, and secondly, to check the separate determinations of income and expenditure.

As has been previously mentioned, the amount of energy received into the body can be determined if we know the amount of the organic constituents of the food and the heat which they develop on combustion; and at the same time it has been stated that for only a few of the alimentary substances has this heat of combustion been accurately determined. We must therefore rest satisfied with estimating the kinetic energy corresponding in a given time to the potential energy at the disposal of the body, and comparing it with the actual amount of energy given out.

The former of these data is estimated according to the following principle: every manifestation of energy is necessarily associated with a corresponding consumption of oxygen, and the consumption of oxygen is, if estimated for long periods of time, equal to the oxygen received into the body (see p. 157). From the oxygen received we might calculate the amount of energy which becomes kinetic, if the whole of the oxygen were used up in the oxidation of one and the same body, whose heat of combustion were exactly known.

Since different compounds of unequal heats of combustion are oxidized, the knowledge of the amount of oxygen received cannot be utilised. But from the oxidation-products which are excreted in a given time we can, at any rate approximately, determine the elements which are oxidized, as for instance, the carbon from the carbonic acid, and the hydrogen from the water, produced in the course of oxidation. The amount of water which is formed in the body can, however, scarcely be estimated, and we are therefore compelled to subtract the amount of oxygen which corresponds to the carbon (*i.e.* required to oxidize

the carbon to form CO_2), and assume that all the remaining oxygen is employed in the oxidation of hydrogen. The error doubtless arising from this dogmatic assumption becomes insignificant when compared with the much larger one, due to our determining the heat of combustion of the carbon and hydrogen found, as equal to the heat which is developed by the combustion of their organic combinations.

As we should expect from these considerations, such researches (as those of Dulong and Despretz) have led to no agreement between the expenditure of heat as calculated and as directly measured.

An attempt has been made to determine, in the case of the energy of the body as in that of its matter, by what channels its distribution is effected. The numbers which have been obtained by calculation, being affected by numerous errors, which have in part been already mentioned, need not be quoted; the results of these calculations possess therefore only the value which attaches to an approximate estimate. According to Barral's calculations the expenditure of the energy of the body is distributed as follows: from 1 to 2 per cent. is lost in heating the excreta (urine and fæces), 4 to 8 per cent. is lost as heat in the respiratory processes, from 20 to 30 per cent. is used up in the evaporation of water; the greatest part (60 to 75 per cent.) leaves the body either as heat conducted or radiated from its surface, or is converted into external mechanical work. (Concerning the importance of this question consult the succeeding section.)

Influence of the Conversion of Energy on the Exchanges of Matter.

In the preceding chapter it has been shortly stated that the oxidation-processes of the body must necessarily reach a certain amount in order that the organism may continue to exist, and that this amount constitutes the 'minimum exchange of its matter.' A closer investigation into the causes which render this minimum exchange necessary reveals at once that the necessary oxidation-processes are required for the supply of the energies of the body, viz. for the development of heat, for the performance of certain kinds of mechanical work (as for the movement of the heart, the movements of respiration, of the

alimentary canal, &c.). The minimum exchange of matter is, therefore, so to speak, conditioned by the minimum exchanges of energy required.

The oxidation-processes which go on in glands appear to constitute an apparent exception to this statement; here, at first sight (see the Introduction), the formation of oxidation-products (the specific constituents of the secretion) would appear to be more important than the evolution of kinetic energy (development of heat) which is associated with it, but there are no proper grounds for such speculations as to uses. For the requirements of the body, not merely the liberated energy, but likewise the chemical products which are the results of the activity of glands, are of use : that which is true of glands is true of the tissues generally, the oxidation-products of which (specific constituents of the tissues) as well as their energies, are utilised.

An increase in the activity of one of these processes must necessarily lead to an increase in the other. It has been already mentioned that an increase of the luxus-consumption increases the kinetic energy of the body, and the case has now to be considered in which an increased expenditure of energy renders an increased consumption of food necessary.

We know by experience that the mechanical work of the muscles, which we shortly designate *work*, is that act of the body associated with transformation of energy, which is most frequently, and to the greatest extent, influenced by the will, by reflex action, by cramps or convulsions due to disease, &c.

An increase in the amount of this work is associated with increased exchanges of matter, and consequently leads to an increase in the excretions, especially to an increased excretion of carbonic acid, and necessitates, if the weight of the body is to remain constant, an increased consumption of food ('Arbeits-Consumption'); at the same time, the sensation which indicates the want of food, viz. hunger, is increased.

It is yet disputed whether, under certain circumstances, especially as a consequence of losses of heat, an increased production of heat takes place in the body, quite independently of muscular movements, but in accordance with certain fixed laws. On this subject the reader must consult the following chapter.

As will afterwards be stated in detail, the different manifestations of energy in the body are associated with the oxidation of specific constituents. In order to form a judgment as to the article of diet which would best supply the increased con-

sumption due to any given act, we should require to know the constituent which principally undergoes oxidation during that act. The most direct way to acquire this knowledge would appear to be to study the organs, as *e.g.* the muscles, in which the various manifestations of energy are observed, and in which the oxidations proceed. As, however, this department of physiology is yet but little developed, we must satisfy ourselves with a study of the changes in the excretions, which correspond to increased evolution of kinetic energy.

Especially has the amount of urea to be studied as evidence of the oxidation of nitrogenous bodies, and the amount of carbonic acid as expressing the oxidation-processes of the body in general.

In consequence of doubtful statements (especially one which asserted that muscular activity increased the excretion of urea) the view was, for a long time, promulgated that only those nitrogenous constituents of the body which enter into the composition of the tissues, are made use of in the production of mechanical work. It was supposed that no heat was developed from these nitrogenous constituents until by processes of decomposition they had furnished non-nitrogenous substances. The non-nitrogenous constituents, on the other hand, were supposed to be simply employed in the production of heat.

Upon these hypotheses was based a classification of foods, according to their uses. The nitrogenous constituents were, because of their relation to the tissues, called 'plastic' (or 'flesh-formers'); the non-nitrogenous, on the other hand, were called 'respiratory' constituents; or, the former were designated as the sole generators of movements, 'dynamogenous,' or 'kinesogenous,' whilst the latter, as the sole generators of heat, were spoken of as 'thermogenous' (Bischoff and Voit). Since it has been ascertained, however, that the excretion of urea is not increased during mechanical work, this hypothesis has fallen to the ground; and the importance of the numerous considerations opposed to it is now fully recognised.

Amongst these the following must be mentioned (M. Traube): 1. That even with a food which is very poor in nitrogen (vegetable food) a considerable amount of mechanical work can be performed (the majority of beasts of burden are herbivorous, and bees, though fed merely on honey, are continually in

motion). Such facts as these could only be brought into harmony with the old theory, by supposing that the mechanical work of the body, even when it attains a high magnitude, is insignificant in amount when compared to the heat formed— a view which has already been combated. 2. That cold-blooded animals, and even animals and men inhabiting hot zones, and whose heat-production can only be very small, yet live, in great part, on a vegetable diet containing but little nitrogen. 3. That carnivorous animals, in spite of the small quantity of non-nitrogenous food which they consume, have sufficient heat generated within them, even when they do not perform much mechanical work. 4. It has lastly been directly ascertained that the albuminous bodies which are consumed in a given time (calculated from the amount of urea excreted) are not by any means capable of accounting for the work done during the same time, even when the heat of combustion of those bodies was calculated extravagantly high (Fick and Wislicenus). With this fact the circumstance is in harmony that the inhabitants of mountainous districts prefer to take fat and sugar as provisions when they have arduous journeys to perform.

We cannot, therefore, point out any act accompanied with the evolution of kinetic energy, for which the consumption of a particular kind of food (nitrogenous food) is absolutely necessary.

CHAPTER VII.

ON THE DEVELOPMENT OF THE HEAT AND ON THE TEMPERATURE OF THE BODY.

I. DEVELOPMENT OF HEAT.

But little remains to be said concerning the origin of the heat of the animal body. It has been repeatedly stated, that in all organs in which processes of oxidation occur, either the whole of the energy which becomes kinetic, or, at least, a considerable fraction of it, takes the form of heat. The other forms of energy (mechanical work, electricity) are only generated in certain organs, and then only in addition to heat.

According to recent investigations even the lungs belong to the group of heat-generating organs; in the lungs the combination of oxygen with hæmoglobin is a source of heat.

The absolute amount of heat generated in the unit of time, by the unit of weight of any organ, is as yet undetermined; it varies greatly, however, in the case of different organs. The glands, for example, generate far more heat than the parenchymatous tissues, because the oxidation-products of the former (the specific constituents of the secretion) are continually being removed and replaced by newly-formed substances. The oxidation-products of the latter, on the other hand, *i.e.* the specific constituents of the parenchymatous juices, remain very long in the place where they originate; oxidation is therefore far more active in glands. Even in one and the same organ the development of heat varies very materially at different times, and, as is readily conceivable, with the energy of the oxidation-processes, or, which is the same thing, with the amount of oxygen which is consumed.

The increased generation of heat dependent on the energy

of the oxidation-processes is particularly remarkable in the case of glands, the temperature of which notably increases as the secretion becomes more active. Even in muscles an increased development of heat is observed during activity. (Consult the following chapter.)

No heat is generated in the horny tissues of the body, in which, it would appear, no oxidation-processes occur. Whether heat is generated in the blood can only be determined by answering the question as to whether oxidation goes on in that fluid.

In addition to the direct sources of heat which have just been referred to, there are also others which have been previously treated of. It has, namely (p. 219), been ascertained that in the body when it is at rest, other forms of kinetic energy, particularly mechanical work, are almost entirely converted into heat. This conversion into heat occurs partly through the friction of the actively moving organs (muscles) against the tissues with which they are in contact, and partly by the friction and dragging of passive organs (tendons, bones, blood in the vessels, &c.) brought about by those which are in active motion. Thus, in the body which is doing work, a great part of the mechanical work is, by friction, converted into heat.

Muscular work consequently increases the production of heat in the body, in a twofold manner: 1. By increasing that production of heat in muscle which is connected with muscular activity. 2. By the friction of the muscle and of the structures moved by it against the surrounding parts.

It is yet undecided whether the production of heat in the parenchymatous tissues (considered apart from glands and muscles) is directly under the control of special nerves. The majority of the changes in temperature which follow the section or the irritation of nerves can be explained by the influence exerted upon the distribution of heat through the vaso-motor nerves (see below). Still, some recent observations appear to point to a direct influence exerted by the nervous system upon the production of heat.

Under certain circumstances, after traumatic lesions which interrupt the continuity of the spinal cord, or after its division (Brodie, Billroth, Quincke), a rise in the temperature of the body occurs. Seeing that division of the spinal cord would by its influence on the vaso-motor nerves cause a lowering of the

temperature, the rise which occurs under such circumstances has led to the supposition that certain fibres exist in the spinal cord which have a direct influence on the production of heat, being capable of inhibiting it. The inhibitory centre presiding over these nerves would, according to this theory, have to be sought for in the brain (Naunyn and Quincke). In order that rise in temperature may occur after division of the spinal cord, the counterbalancing influence exerted by the vaso-motor nerves must be prevented, by hindering the external loss of heat. Some have failed to observe any rise of temperature as a consequence of division of the cord (Rosenthal).

Even when the medulla oblongata is separated from the pons Varolii, and when both the portions of the brain are injured, rises in temperature occur (Tscheschichin, Bruck, and Günther) which cannot yet be adequately explained.

II. TEMPERATURE OF THE BODY.

The different organs of the animal body are in relation with one another, in part by actual contact, and in part through the circulating blood, which acts as a conductor or distributor of heat. Through its agency, the heat generated in the different parts of the economy is distributed pretty uniformly throughout the body, and even to those parts of it which do not themselves generate heat. The result of this equalisation, as well as of the losses of heat about to be discussed, is an approximately constant temperature of the whole body, which in the human subject varies between 36° C. and 38° C. The temperature is nearly the same in other mammals; it is higher in birds. Organisms which possess a constant temperature are called *warm-blooded* or homo-thermous. In other animals the energy of the oxidation-processes, and consequently the heat generated, is so small in amount, that there is no constant body-temperature, which merely rises a few degrees above that of the surrounding medium (air or water). Such animals are called *cold-blooded* or, more appropriately, poikilothermous (of variable temperature).

Losses of Heat.

The animal body, being almost always surrounded by media which are colder than itself, is constantly giving out heat to

them. This loss of heat occurs in the following manners: 1. *By radiation* from the free surfaces of the body. 2. *By conduction.* *a.* To those bodies which are in contact with the surface and are colder than the body, especially air and clothing. *b.* To the bodies taken into the organism, air and food, which are colder than it. The last-named loss of heat is frequently expressed by saying, that the body gives up heat with its excreta (expired air, sweat, urine, fæces), which possess, in general, the temperature of the body. • Obviously these are two ways of expressing the same facts, assuming, as is generally the case, that the matters taken into and excreted from the body are equal in quantity and possess the same specific heat. *c.* To excreta, especially sweat, which have to be evaporated, and which, during evaporation, remain in contact with the surface of the body; the heat thus given up becomes forthwith latent. It is usual to express this loss of heat as ' heat lost by the evaporation of water.'

As the loss of heat takes place principally from the surface of the body, its amount depends upon the extent of that surface; and it is therefore clear that small individuals, the external surface of whose body, as compared with their body-weight, is more extensive, give up relatively more heat to the medium which surrounds them than do larger ones.

Many of the losses of heat here referred to are of very variable nature; and their variability is utilised in maintaining the constancy of the temperature of the body.

Local Temperatures.

For reasons which are easily intelligible, the above-mentioned equalisation between the temperatures of the different parts of the body cannot be complete, so that certain differences in temperature constantly exist. These differences, which, without any further explanation, may be surmised from the relations of the body already alluded to, have by experiment been fully determined to exist; they are principally the following: 1. The greater the amount of heat which any part of the body generates, the warmer it is (*cæteris paribus*). Glands are, therefore, hottest during secretion, and muscles during work (and during *rigor mortis*); the horny (epithelial) tissues are the coldest. 2. The greater the amount of heat which any

organ must lose by radiation or conduction, in consequence of its situation or of other relations, the colder it is.   Hence the following structures are the coolest: the skin, particularly when it is covered with sweat; the lungs; the first portions of the alimentary canal; &c.   3. Amongst these parts of the body, those are coldest which are most exposed, those warmest which are most protected (*e.g.* the axilla, the cavity of the mouth, &c.).   As the blood is the most important agent in the equalisation of the•temperature of the different parts of the body, its temperature might be taken as representing the mean temperature of the body; as a fact, the numbers which have been given at page 228 are deduced from observations of the heat of the blood.   From the facts stated we may further conclude: *a.* In organs which generate much heat, and whose temperature therefore exceeds that of the blood (glands, muscles during work), the venous blood which flows out of them is warmer than the arterial blood which flows into them; the· opposite is the case with organs which produce little heat or which give up heat to the external medium; thus, for example, the venous blood of the skin is cooler than the arterial.   According to some observers (Colin, Jacobson, and Bernhardt), the heat which the blood in the lungs loses to the air is more. than compensated for by the combination with oxygen, so that the blood of the pulmonary veins and of the left side of the heart is hotter than that of the right side of the heart.   According to others, however (G. Liebig, Bernard, Heidenhain and Körner), the opposite is the case; a fact to be explained, according to Körner, not by the small losses of heat sustained in the lungs (p. 151), but by the fact of the thin-walled right side of the heart lying near the warm abdominal viscera in its vicinity.   *b.* An organ whose temperature is below that of the blood becomes *warmer* in proportion as the amount of blood flowing into it in the unit of time increases.   The temperature of such organs (as the skin) increases under the following circumstances:—when the blood-pressure of the whole body is raised; when the activity of the heart is increased; and particularly when the arteries supplying them are dilated (as when their vaso-motor nerves are divided).   On the other hand, under opposite circumstances, the temperature falls.   Hence, redness

of any portion of the skin is, as a rule, accompanied by heat, paleness by cold.

Even the heat of inflamed parts merely depends upon a more active supply of blood to them, and not upon an ncreased local production of heat, as it is constantly lower than the normal temperature of the internal organs (Hunter, Jacobson and Bernhardt, Schneider).

These relations must always be kept in mind in determinations of the temperature of the body as a whole. As it is only in the case of the lower animals that the temperature of the blood can be directly determined by placing thermometers in the vessels, in man those parts are chosen for observation of temperature which are least exposed to loss of heat; the thermometer is therefore placed in the cavity of the mouth, in the rectum, in the vagina, or in the axilla, and is allowed to remain there as long as possible. It must here be mentioned that a high temperature of the external zone of the body, by increasing the loss of heat, leads to a cooling of the interior. Conclusions cannot, therefore, be safely drawn from determinations of the temperature of the external zone as to the temperature of the interior of the body; the latter can be determined by placing the thermometer deeply into the rectum. Absolute determinations of temperature are always made with the (mercurial) thermometer. Comparisons of the temperature of two parts of the body, or of the temperature of the same part at different times and under different conditions, &c., are conducted either with the aid of the thermometer, or better still, by thermo-electric methods (Chapter VIII.).

Maintenance of the Mean Temperature in Warm-blooded Animals.

The mean temperature which has been stated to exist in man and warm-blooded animals appears to be an absolutely necessary condition for the most important vital processes.

This conclusion is arrived at by a consideration of the fact that even small deviations of the temperature of the body beyond the stated limits (36° C. to 38° C.) are accompanied by important dangers. The numerous processes which go on in the body, and which are akin to fermentation, explain these dangers ; at a temperature of 42·6° C. coagulation within the blood-vessels commences (Weikart), and at 49° C. heat-rigor commences in the muscles (Chapter VIII.). Accordingly the organism possesses numerous contrivances for maintaining its temperature within certain limits.

The most important of these are the following :—

1. Such arrangements as act by regulating the amount of heat *eliminated*: *a.* The sensation of a diminished or increased temperature (sensation of cold or heat, Chap. X.) leads man in the first case to surround himself with bad conductors of heat (thick clothes, wool, silk), and in the second with good conductors (thin clothes, linen), or even to use extraneous means (cold baths), to get rid of some of the body heat. *b.* Increased temperature increases the activity of the heart (p. 80) and of respiration (p. 167); the former leads to an increased fulness of the capillaries, amongst others of those of the skin, and consequently to a rise in the temperature of the latter organ, and to an increased loss of heat by conduction and radiation. Thus, when the heat of the body increases, the skin becomes turgid, warm, and moist; when the temperature falls, on the other hand, the skin shrinks, and becomes cold and dry. Increased respiratory activity augments the loss of water from the respiratory passages.[1] The secretion of sweat is, moreover, either occasioned or increased in quantity by an increased fulness of the vessels of the skin, and the rapidly evaporated sweat consumes an extraordinary amount of heat. In summer, when the surrounding air is of nearly the same temperature as the body, this is almost the only way in which the heat of the body is lost. *c.* Cold causes contraction, and heat causes dilatation of the small arteries (p. 75), especially of the skin. This must exert the same regulating action as the phenomena referred to under *b.*

2. Such arrangements as exert their action in regulating the *production* of heat: *a.* An involuntary and direct increase in the amount of heat produced on exposure to cold, which takes place in a manner yet unknown, has been suspected to occur by some (Hoppe, Liebermeister, Röhrig and Zuntz), especially because under the influence of the cold bath the temperature of the axilla at first rises, whilst the excretion of carbonic acid is increased; others, however (Senator, Winternitz), suppose the first phenomenon to be due to an arrested loss of heat owing to the contraction of the blood-vessels of the skin, whilst the increase of tissue-change, evidenced by the increase in the

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[1] The possible generation of heat in the lungs cannot be materially increased by increased respiration without a corresponding increase in the quantity of oxygen used.

excretion of carbonic acid, is not a constant phenomenon, and may be replaced by a decrease ; in any case it need not be associated with an increased production of heat. *b.* A diminution of temperature (cold) increases the feeling of hunger, and increased consumption of food augments the production of heat. *c.* When the body is exposed to cold the need for muscular exertion is felt,—such as walking backwards and forwards, work—and this raises the temperature in a twofold manner (p. 227); further, there occur certain (presumably reflex) involuntary muscular movements (shivering, chattering of the teeth), both of which actions can be executed voluntarily with the object of generating heat.

Small individuals, whose losses of heat are constantly greater than those of larger individuals, eat more and move more actively.

The efficiency of the regulating arrangements in providing against loss of heat, especially in the case of man, is but small, so that clothing, fuel, and movements of the body are the most efficacious protection which he possesses against the cold.

Fluctuations in the Mean Temperature.

It yet remains to be stated that fluctuations of the mean body temperature (blood-heat) occur within the normal limits, *i.e.*, within such limits as not to call into action the regulating apparatus of the body ; and further, to point out what relation these fluctuations bear to the functions of the body and the mode of living. As the heat-producing processes, as a whole, yield carbonic acid nearly in proportion to the heat generated, the fluctuations of heat coincide very nearly with the fluctuations in the carbonic acid excreted.

The following circumstances cause a high temperature :— muscular movements ; abundant glandular secretion, especially of bile (hence the calorific value of digestion); great energy of the whole material exchanges of the body, as in persons of the male sex, of strong constitution, of adult age, &c. ; morbidly increased material exchanges, such as probably exist in fever (the excretion of urea is here increased, and before the rise in temperature occurs, so that the former phenomenon cannot (p. 214) be explained by the latter, Naunyn). Circumstances of an opposite nature to the above often cause low temperatures, as do also diseased conditions, which restrain the consumption of oxygen (such as some diseases of the lungs, starvation, p. 207), &c.

Further, a diurnal fluctuation of the temperature of the body occurs, independently of the digestive process, which appears to be due to variations in the energy of the oxidation-processes connected with particular periods of the day.

Not only can the mean temperature of the body be affected in a lasting manner by the processes which generate heat, but likewise by those concerned in its dissipation from the body: thus, *e.g.*, the body-temperature is very much influenced by the state of contraction of the blood-vessels of the skin, and therefore by the state of excitation of the vaso-motor centre ; as the latter is increased in fever, the high temperatures of fever may in part be thus explained (L. Traube).

The heat of the blood diminishes when sensory nerves are irritated (Mantegazza, Heidenhain), apparently through the agency of the medulla oblongata; for when the medulla is excited directly the same results follow.   This effect is due to an acceleration of the blood current and a consequently increased loss of heat (Heidenhain).

From the facts which have been stated it is easy to explain the increase of temperature which follows irritation of the spinal cord (Tscheschichin), and the decrease caused by division of the spinal cord, as well as by paralysis of the vaso-motor nerves brought about by poisons (nicotine, curare). We conclude that an increased elimination of heat does take place in the latter circumstances from the fact that when the animals subjected to experiment are placed in a warm medium, section of the spinal cord (according to some authors, p. 227 *et seq.*) leads to a rise in temperature.

Hybernating animals possess during the period of hybernation a very low temperature.   In them the production of heat, as well as the loss of heat, is reduced to a minimum, by an extraordinary slowing of the circulation.

Ordinary warm-blooded animals die when exposed to cold, so soon as their temperature has sunk below a certain limit. Previous to death in them, as in hybernating animals, the frequency of the pulse and the movements of the alimentary canal undergo an enormous diminution, and the central nervous organs become incapable of performing many actions, as *e.g.* of bringing about the convulsions of asphyxia (Horwath).   If the temperature of the body does not fall below the limit indicated above, the animal may by warmth be awakened from the soporific state into which it has fallen, and which corresponds to the winter-sleep of hybernating animals.   If the cooling does not cause the body-temperature to fall below 20° or 18°, the animals possess the means of warming themselves again, as soon as they are rought from the cold into a mean temperature.   Even when the diminution of temperature has exceeded these limits, the body can of itself become

warm again, if artificial respiration be carried on (Walther; Horwath succeeded in reviving animals, whose bodies had been cooled to 5° C., by merely warming them).

APPENDIX.

Immediately after death a temporary rise of temperature is frequently observed (post-mortem rise in temperature). According to some this rise is due to the formation of heat which attends rigor mortis, whilst others account for it by supposing that when the circulation ceases, whilst the loss of heat is very materially delayed, the production of heat in the different organs continues for some time after death (Heidenhain).

CHAPTER VIII.

THE ENERGY OF MECHANICAL WORK (MOVEMENTS OF THE BODY).

THE liberation of energy in the form of motion is far less frequent in the animal body than the formation of heat, and is connected with certain definite apparatuses. These apparatuses are, wherever found, simple or metamorphosed cells, or constituents of cells. The phenomena of motion have been proved to occur in the following situations in the human body : 1. In muscular fibres, striated and smooth. 2. In lymph-corpuscles and the corpuscles resembling them (colourless blood-corpuscles, connective-tissue corpuscles, mucus-corpuscles, pus-corpuscles, etc.). 3. In ciliated cells. 4. In spermatozoa. 5. In cells exhibiting molecular movements. To these must be added the contractile masses of many simple organisms. Finally, the processes of formation, growth, division, etc., may be regarded as movements. The movements previously mentioned are, however, contrasted with those just given by their much greater rapidity, which renders their direct observation possible ; whereas the processes of growth take place so slowly as to be only recognisable, after considerable intervals, in their effects. The former, also, cause only transitory changes of place and form, after which the parts set in motion return approximately to their previous condition ; while the latter lead to permanent alterations. The latter are referred to in the fourth Section of the work.

The above-mentioned organs, some of which are entirely, and others in part, contractile, have, as far as they have been investigated, certain characteristics in common, apart from the contractility itself, which point to an essential substance present in all. This substance appears throughout the animal kingdom, and in many vegetable organisms. It was formerly termed 'sarcode ; ' but now in general it is called 'protoplasm.' It may, therefore, be stated as a general law, that active movements only occur where proto-

plasm is found. The properties of protoplasm will be most fittingly described in connection with the physiology of the most important and most thoroughly investigated of the motor apparatuses of the body, viz. the muscles, which will now be considered.

I. THE MUSCLES.

Muscles are essentially distinguished from almost all other motor-structures by the fact that in them motion only occurs after the operation of a liberating force, the existence of which may be demonstrated. This liberation originates, as a rule, in the nervous system.

The existence of automatic muscular movements has been recently maintained (Engelmann: see Smooth Muscle).

Two kinds of muscles are distinguished, chiefly from the arrangement of their histological elements, viz., the striated and the smooth. The physiological properties of both are, as the following consideration will show, essentially the same, although many distinctions appear in the details.

A. *Striated Muscles.*

Transversely striated muscles are placed wherever energetic movements occur. With few exceptions all such movements, and consequently the activity of all transversely striated muscles, are dependent upon the will. Striated muscles are therefore also called voluntary muscles. The heart, whose striated fibres differ in other respects also from those of ordinary voluntary muscle, forms the chief of the exceptions (p. 56).

Striated muscles form for the most part long roundish cords, or sometimes flat expansions, of a reddish-brown colour, which exhibit a coarse longitudinal fibrillation. They are attached to the parts to be moved (bone, cartilage, etc.) either directly or by means of bundles of connective-tissue (tendons). They are surrounded by strong sheaths of connective-tissue (fasciæ); and internally they are divided up into numerous longitudinal bundles by septa of a finer connective-tissue (perimysia). A piece of muscle may without difficulty be teased and separated in a longitudinal direction into smaller and smaller bundles of

fibres, until what is called the '*primitive bundle*' is reached, after which separation by tearing is impossible. This 'primitive bundle' is really no bundle at all, but a tube filled with an apparently fluid mass—the proper muscular substance. The wall of this tube (the *muscle-fibre* or *muscle-tube*) consists of a very elastic, completely closed membrane—the *sarcolemma*. The contents exhibit under the microscope fine, regular *transverse striæ*, caused by rows of little bodies possessing more strongly refractile properties than the ground-substance. These little bodies are doubly refractive (Brücke). The distance between the transverse striæ, while the muscle is at rest, is very regular, and differs little in the various classes of animals (0·0020 to 0·0028^{mm}) (Hensen). The majority of the muscle-tubes run the whole length of the muscle, and are attached directly to the tendon, bone, etc.; some, however, end in pointed extremities in the interior of the muscle (Rollett).

It is concluded that the contents of the muscle-tubes are fluid from the fact that, under certain circumstances, waves of motion are seen travelling along them; and especially from the appearance here, as in other fluids, of Porret's phenomena (Kühne), *i.e.* the flow of the contents towards the negative pole on the transmission of an electric current through a muscle-tube. One observer (Kühne) has, moreover, seen in a recently prepared specimen of frog-muscle an included nematode worm move about evidently without any mechanical resistance. Under the influence of various reagents, the contents of the muscle-tubes solidify (as will be described more fully hereafter) and fall to pieces in various directions: *a.* in the direction of the transverse striæ, into round thin plates ('discs,' Bowman); *b.* in a longitudinal direction, into fine longitudinal fibres which exhibit slight varicose swellings at distances corresponding with the intervals of the striæ in the fresh condition of the muscle, constituting, therefore, an indication of the earlier striated condition (muscular fibrillæ, Kölliker); *c.* in both directions at once, into small prismatic bodies which may be regarded as due to the breaking up of the fibrillæ in a transverse direction, or of the discs in a longitudinal direction ('sarcous elements,' Bowman; 'muscle-prisms,' Kühne). All these structures formed by the splitting up of the 'primitive bundle' or 'muscle-tube' have, at one time or another, been regarded as pre-formed muscular elements. Now that a more accurate knowledge of facts has rendered it possible to regard the sarcous elements of living muscle (especially of the muscles of insects) as bodies suspended in the fluid contents of the muscle-tube, we must consider the sarcous bodies as pre-formed elements, the fibrillæ as a row of those elements superimposed, and the discs as made up of a number placed side by side in one plane. In most muscles the sarcous elements have the property, on coagulating, of separating in such a manner as to form fibrillæ; and many reagents have the power of splitting muscle-tubes into discs. The sarcous elements exhibit for the most part on

section from three to five sides, and they are so closely apposed that there exists but a small space between them for the fluid ground-substance (Cohnheim).

When examined with polarised light, the sarcous elements appear doubly refractive (and coloured, with crossed Nichol's prisms), while the ground substance refracts light simply. As they change their form during contraction, becoming shorter and thicker, they cannot be regarded as simple doubly-refractive structures, like crystals, but must be supposed to consist of groups of numerous small doubly-refractive elements (' disdiaclasts '), which are arranged differently in sarcous elements at rest and in contraction (Brücke).

According to more recent views (Krause, Hensen, Flögel, Merkel, Engelmann, and others), over the details of which there is, however, yet much dispute, the structure of muscular tissue is much more complicated than that which has just been given. The transverse striation is the optical effect of the alternation of light and dark layers; in the middle of the bright striæ a fine line is seen, which is taken to indicate the existence of a transverse membrane (Krause). In the dark layers also a (bright) transverse line is described. New schemes of construction have been built upon these discoveries, into the consideration of which we cannot enter here, as it is very difficult to exclude the differentiating effects of post-mortem coagulation. Krause's scheme is the most complicated, in which the sarcolemma is divided up, by means of transverse and longitudinal septa, into a system of ' muscle-cells,' each of which contains a sarcous element forming part of the dark transverse line existing between the two brighter, fluid layers which are in contact with the transverse septa.

In addition to the above, muscle-tubes contain the following morphological elements :—

1. Nuclei. These are cellular, with nucleoli surrounded by a shapeless mass of granular matter (which is regarded by some as protoplasm); they lie in the neighbourhood of the sarcolemma, but in many animals they are scattered regularly throughout the contents of the muscle-tubes.

2. Nerve-terminations (Kühne). The branched primitive nerve-fibres enter the muscle-tubes, the neurilemma becoming continuous with the sarcolemma; the white substance of Schwann ceases immediately after entrance, and the axis-cylinder passes into a prominence, or mass of matter, lying immediately upon the transversely striated substance of the muscle-tube and called the terminal nervous prominence, or prominence of Doyère—the sarcolemma being bulged outwards at that point: The substance composing this prominence of Doyère is homogeneous, finely granulated and provided with large nuclei in which lies a forked expansion (terminal plate), the proper termination of the axis-cylinder. For every nerve-fibre which enters a muscle there are, in the muscles of the eye, one to ten muscular fibres, and in other muscles far more, as many as twenty to eighty (Tergast).

Muscles have, in addition to muscle-tubes and the septal system of the perimysium, an abundant supply of connective-tissue connected with the latter, as well as blood- and lymph-vessels, and a network of nerves.

The Chemical Constituents of Muscle.

The reaction of fresh muscle in a state of repose is neutral, or, owing to its being moistened with alkaline juices (lymph), slightly alkaline (du Bois-Reymond).

As muscle is chemically a very unstable substance, the determination of certain of its constituents requires special precautions, and is not yet complete. Such are, in particular, the albuminous constituents. The contents of the muscle-tubes may be obtained as pure as it is possible to obtain them by the following methods (Kühne): 1. By expressing the juice from the muscles of cold-blooded animals after first removing the blood by washing out the vessels with some indifferent fluid (·5 to 1 per cent. solution of NaCl). 2. By freezing bloodless muscles, separating them into small fragments by means of cooled instruments, and allowing them to filter at a temperature slightly above 0° C., the latter operation being assisted by the previous addition of cooled NaCl solution. The '*muscle-plasma*' so obtained is a turbid, neutral or slightly alkaline fluid. It undergoes change more or less rapidly according as the temperature is higher or lower. It coagulates, firstly forming a homogeneous gelatinous mass, coagulation being recognisable only by the fact that the plasma becomes tougher and cannot be poured from the containing vessel; but afterwards the coagulum contracts into flocculi, in the course of which it becomes very turbid and liberates an acid fluid, '*muscle-serum.*'

The body thus separated in the process of coagulation is an albuminous body, *myosin.* It is soluble in concentrated NaCl-solution, and is precipitable from such solutions by the addition of more water or more salt. Dilute acids also easily dissolve myosin, and, in doing so, convert it into syntonin (p. 32).

Spontaneous separation of myosin takes place most rapidly, indeed instantaneously, at a temperature of 40° C. for cold-blooded animals, and of 48°–50° C. for warm-blooded animals. It may also be induced at once by means of distilled water and acids.

The muscle-serum contains the remainder of the constituents, viz.: 1. A number of albuminous bodies which coagulate at various temperatures from 45° to 70° C., that coagulating at about

60° or 70° being ordinary albumin. 2. Various carbo-hydrates: viz. (a) glycogen (Nasse), which is present in especially large quantities in embryos and young animals (Mac-Donnell); (b) the products of the decomposition of glycogen—dextrin (Limpricht), and grape-sugar (Meissner), which are said by Nasse only to appear *post mortem*; (c) inosite, in large amount. 3. Lecithin in all probability, on account of the presence in muscles of the terminations of nerves; this has not, however, been directly proved. 4. Fats in small amounts. 5. Free acids, especially sarcolactic acid, in addition to certain volatile fatty acids—formic, acetic. 6. Various amides: viz., creatine (and, according to some, creatinine also, though others incline to the belief that the latter is derived directly from the former), carnine (p. 27), hypoxanthine (sarcine), xanthine, inosinic acid, and sometimes uric acid, though this is doubtful. 7. A red colouring matter,—in most muscles hæmoglobin (Kühne). 8. Salts, especially salts of potassium. 9. Water. 10. Gases, chiefly carbonic acid.

The above-named constituents are those of the contents of muscle-tubes which have already undergone coagulation. As the latter process, as well as contraction (see below), is connected with certain chemical changes in the muscle which are as yet imperfectly understood, and as the investigation of uncoagulated muscle or muscle-plasma cannot be carried on without the occurrence of this process, the substances just mentioned are not to be regarded as the constituents of unaltered living muscle. All that has been discovered or surmised with respect to them will be stated in the proper place.

In muscle as a whole there are found, in addition, the constituents of the other bodies which help to make up the structure (connective-tissue, vessels, blood, nerves, &c.). Gelatigenous substance, elastin, &c., must, therefore, be added to the above list. The sarcolemma appears to consist of an elastic substance.

The quantitative composition of coagulated beef-muscle is as follows (Lehmann): in 100 parts—water, 70–80; solids, 26–20; insoluble albuminous bodies (among them myosin, the sarcolemma, &c.), 15·4–17·7; soluble albuminous bodies, and alkaline albuminate of potassium, 2·2–3·0; gelatin, 0·6–1·9; creatine, 0·07–0·14; fat, 1·5–2·3; lactic acid, 1·5–2·3; phosphoric acid, 0·66–0·7; potassium, 0·5–0·54; the remainder of the ash, 0·17–0·26. Carnine has hitherto only been found in the extract of beef (1 p.c. in Liebig's extract, Weidel).

Conditions of Muscle.

The usual condition of living muscle is one of rest; the processes taking place in muscle in such a state are imperceptible except by the aid of delicate instruments. Out of this state of rest muscle may pass, under certain conditions, into other states: 1. Into a state of activity, during which a visible shortening of the muscle occurs. 2. Into a state of rigor, which is induced by certain chemical changes connected with the cessation of life (coagulation), and which, also, is accompanied by a diminution in length.

a. **Muscle in a State of Rest.**

Mechanical Properties of Muscle in a State of Rest.

For the sake of simplicity we shall regard all muscles here as spindle-shaped, and extended in the direction of their length —a form which the majority of muscles have in fact. A muscle is a structure of slight but very perfect elasticity, *i.e.* it is very extensile, slight weights producing a considerable elongation; but it has the power of returning, immediately on the removal of the extending force, to its original length. During elongation there is, of course, a diminution in thickness, but the volume remains about the same (it is said to be slightly diminished—Schmulewitsch). Unlike inorganic bodies, and resembling in this respect all other organic structures, muscle does not elongate proportionately to the extending force; but equal increments of extending force produce a less amount of elongation the greater the degree of tension of the muscle at the time (Ed. Weber). The curve of extension got by taking the weights as abscissæ and the degree to which they extend the muscle as ordinates is, therefore, not a straight line as in the case of inorganic bodies, but approaches an hyperbola (Wertheim). In the living body the muscles are constantly stretched a little beyond their natural length, as is shown by their retraction from their point of attachment when the fibres are cut across. The value of this lies in the fact that, on contraction, the points of attachment and insertion are approximated immediately without any loss of time or energy in

gathering up, or rendering taut, the relaxed muscle. In muscles separated from their attachments the muscle-tubes are not usually found extended in straight lines, but in curves and zigzags.

Exchanges of Matter in Muscle in a State of Rest.

Very little has yet been discovered respecting the chemical processes taking place in resting muscle. As muscular tissue continually effects the conversion into venous blood of the arterial blood flowing to it, chemical processes must occur in it, in which oxygen is used and carbonic acid formed. Certain observations which will be detailed afterwards render it probable that these processes (viz. the use of oxygen and the formation of carbonic acid) are not identical, but only take place side by side.

In excised muscles (and here it is best to use those of cold-blooded animals, as they retain for a long time the properties of normal living muscle) an absorption of oxygen and an excretion of carbonic acid may be detected (du Bois-Reymond, G. Liebig); as also in muscles which have been deprived of blood (p. 240). These operations cannot therefore be ascribed to the blood in the blood-vessels of the muscle, but to the muscular substance itelf. As the same gaseous exchanges are exhibited by muscle in a state of rigor as by living muscle (Hermann), they cannot, at least in by far the majority of cases, be considered as the result of functional processes, but must be regarded as due to putrefactive changes which occur especially at the surface of the muscle and at the exposed transverse sections. The amount of such gaseous exchanges is in accordance with this theory, being greater the larger the surface of the muscle exposed, and the nearer it is to absolute putrefaction.

As, however, excised muscles retain their vitality under certain circumstances somewhat longer in air or oxygen than in hydrogen or other indifferent gases which contain no oxygen (Humboldt, G. Liebig, Hermann), it must be admitted that some slight absorption of oxygen connected with the functions of the muscle does take place, which is, nevertheless, too small to account for the gaseous exchanges above mentioned. That the physiological absorption of oxygen in muscles through which blood is passing is much greater than in those which are excised, and so removed from the circulation, may be accounted for by the following circumstances: 1. That, in the former case, a much greater extent of surface is exposed to the operation of the oxygen-carrier, viz. the blood, than in the latter, where the oxygen-carrier is the atmosphere and the surface exposed the external superficies. 2. That the oxygen of the blood, which is combined with hæmoglobin, may possibly have special properties more favourable to its transference to the muscular substance than those of the free atmospheric oxygen (p. 47). 3. That, in

the process of combining oxygen with the muscle-substance, other bodies are needed which are not found in muscle itself, but are conveyed to it by the blood.

Nothing further has been directly made out concerning the chemical processes of resting muscle; but certain conclusions may be drawn from the appearances of muscle during contraction and rigor; reference will, therefore, be presently made to this matter.

b. Muscle in Rigor.

If a muscle is removed from the blood-current, or excised from the body altogether, it passes—in warm-blooded animals quickly, in cold-blooded animals much more slowly—into a state which is called *death-rigor.* In this condition it is devoid of irritability, it is strongly contracted in the direction of its length, it is less elastic, it has a whitish curdled appearance, and an acid reaction (du Bois-Reymond); and its volume is slightly diminished (Schmulewitsch, Walker). Under the microscope the previously transparent muscle-tubes appear opaque and flocculent, and their contents solid (Kühne). The force exerted in the contraction of rigor will be spoken of in considering Irritability.

The appearance of 'spontaneous' rigor is hastened by previous continued activity of the muscle; and by heat, a temperature of 40° C. for cold-blooded animals, or of 48° to 50° C. for warm-blooded animals, inducing it instantly (*heat-rigor*). In the cold the occurrence of rigor is much delayed, not taking place for several days at a temperature of 0° C. It is induced, moreover, by distilled water (*water-rigor*), by acids, even the weaker kinds, such as carbonic acid (*acid-rigor*), by various chemical bodies, and by first freezing and then thawing the muscle.

The action of many of the above-mentioned agents in inducing rigor may take place even when the circulation through the muscle is intact; but a longer-continued and intenser operation is necessary. The effect of the circulation of blood through the muscle is to retard the occurrence of rigor (Hermann).

Cessation of the blood-circulation causes rigor in muscle by depriving it of oxygen; for rigor may be postponed for a con-

siderable time in excised muscles by injecting into their vessels oxygenated blood—a result which does not follow if the blood injected contain no oxygen (Ludwig and A. Schmidt). Moreover, excised muscles through which no blood is passed lose their irritability less quickly in air or oxygen than in gases containing no oxygen (von Humboldt, G. Liebig); but here the difference is extremely small, probably because the oxygen comes into contact only with the external surface of the muscle.

The essential process in rigor is a coagulation of the contents of the muscle-tubes, whereby they become solid (Brücke, Kühne). The coagulated body, the spontaneous separation of which from muscle-plasma takes place at once at a higher temperature, is an albuminous substance, *myosin*. From the observations upon muscle-plasma we must suppose that the contents of the muscle-tubes become first viscid and then gelatinous; and that at last the coagulum, like the coagulum of fibrin in a blood-clot, contracts, thus shortening the muscle, which becomes opaque and yields a juice, the *muscle-serum* (p. 240). It appears, therefore, that various stages are to be distinguished in the occurrence of rigor, only the last of which are visible to the eye, viz. the opacity and the diminution in length.

Besides the separation of myosin other processes occur, viz.: 1. The already-mentioned acidification, which is the result of the formation of an acid or of an acid salt. The acid may be sarco-lactic acid (p. 15 *et sq.*); but glycerin-phosphoric acid is also said to be present (Diaconow). The amount of acid which results from the occurrence of rigor in a muscle is the same whether the latter take place slowly (spontaneous rigor) or quickly (heat-rigor) (J. Ranke). 2. An excretion of carbonic acid which depends upon the formation of free carbonic acid. Here again the amount is independent of the method by which rigor is induced. The carbonic acid formed during the occurrence of rigor is, moreover, less the greater the amount the muscle has generated previously by contracting (Hermann). 3. A diminution in the amount of glycogen present, which is also independent of the manner in which rigor takes place: it has not been discovered what becomes of the glycogen (O. Nasse).

Of the first, imperceptible, stage in the separation of myosin, it may be said that, in all probability, in the case of cold-

blooded animals, it takes place very gradually, since a muscle from the moment of its excision, after a very transitory period of exalted irritability, steadily loses its power of responding to stimulation: it may therefore be said that excised muscle commences at once to pass slowly into a condition of rigor, *i.e.* myosin is separated in a gelatinous form, carbonic acid is generated, glycogen is used up, and an acid appears which gradually changes the reaction of the muscle to test paper. The second stage, however, does not occur until after some time, and consists in the contraction of the coagulum and the shortening of the muscle, thus completing rigor. When rigor has become complete the muscle begins to putrefy, in the course of which vibriones are formed, the acid reaction gives place gradually to an alkaline one owing to the formation of ammonia, and ill-odoured gases are given off. Putrefying muscle evolves, even in a vacuum, chiefly carbonic acid, nitrogen, and a little sulphuretted hydrogen. Long before the excised muscle is in rigor in every part, similar, though slighter, putrefactive changes have commenced on its external surface.

A muscle may be reclaimed from the first stage of rigor by allowing blood to flow through its vessels, but not from the second, *i.e.* after the contraction of the coagulum of myosin (Kühne, Hermann). The second stage of rigor may be rapidly induced in the muscle of a warm-blooded animal by ligaturing the arteries conveying blood to it (Stenson), and from this stage it cannot recover by the mere renewal of the interrupted blood-current. More will be said hereafter concerning the nature of this recovery.

By suddenly heating a muscle strongly (as by throwing it into boiling water—scalding) it loses its power of entering into rigor: it neither becomes acid in its reaction under such circumstances (du Bois-Reymond) nor forms carbonic acid (Hermann). Mineral acids have the same effect; and we must therefore distinguish acid-rigor from that which usually occurs (Hermann).

If the muscles remain in their natural position in the body after death, their contraction on entering into rigor produces a stiffness of all the limbs—death-rigor—which does not disappear until the occurrence of putrefaction, after which they again become lax. From this rigor, or stiffening, of the corpse, the term as applied to muscles is derived.

The position of the limbs in the stiffened corpse is chiefly the result of the tension of the muscles and the weight of the limbs. In some cases, when rigor has occurred very suddenly, the limbs have been fixed in the positions they occupied owing to the contraction of their muscles at the moment of death (Rossbach).

c. Muscle in a State of Activity.

That change of state in muscles which is most important, physiologically speaking, is the passage into the active condition, *i.e.* into a condition in which the material exchanges increase, and the muscle takes upon itself a new form.

Liberation of Muscular Activity.

The influences which call forth this change of condition are called *stimuli*; the conversion of the muscle from one state to the other, *excitation*; and the capability of excitation by means of stimuli, which characterizes muscle, its *irritability*. Inasmuch as the stimuli induce the conversion of potential into kinetic energy, they have the relationship to the latter of liberating forces (p. 6), and we may, therefore, speak of the liberation of muscular activity by means of stimuli. The normal stimulus for muscle proceeds from the motor nerves which are scattered throughout its substance; its nature is little understood, and will be discussed in the next chapter. There are, however, numerous other muscular stimuli, some of which are the result of morbid conditions, while others may be employed artificially.

For a long time it was thought that muscles were incapable of direct excitation, *i.e.* that all stimuli applied directly and with effect to muscle only act upon the muscles through the nerve-terminations contained in them. The following circumstances have, however, decided the matter in favour of the independent excitability of muscle. 1. Portions of muscle containing no nerve-endings, *e.g.*, the extremity of the sartorius of the frog, are capable of excitation by means of the direct application of stimuli (Kühne). 2. Certain chemical stimuli are incapable of exciting nerves (Kühne); while, on the contrary, certain electrical stimuli which act upon nerves have no effect upon muscle itself (Brücke: Chapter IX.) 3. Substances which have the property of rendering nerves, and especially intramuscular nerve-endings, inactive, do not deprive muscle of its capability of direct excitation (*e.g.* the Indian arrow-poison—curare, Kölliker). Moreover, other influences (*e.g.* excessive cold, interruption of blood-current) induce a transitory state in which intramuscular nerve-terminations are paralysed while the

possibility of direct excitation remains to the muscles. 4. In certain conditions (exhaustion of muscle) local irritation induces contraction only in the immediate neighbourhood of the point of application of the stimulus, without respect to the distribution of the nerves near the spot (Schiff, Kühne). 5. The lower contractile organisms, which agree in the nature of their essential substance with muscle, are quite destitute of nerves. 6. It is, moreover, said that automatic movements occur in the muscles of the more highly organised animals. (Consult the section on Smooth Muscles).

The muscular stimuli with which we are already acquainted are: 1. *The normal nervous stimulus,* which proceeds to the muscle either from the central nervous organ in the production of voluntary, automatic, or reflex movements, or from some point in the course of the nerve supplying the muscle, at which irritation has been applied. 2. *Electrical stimuli,* which will be more fittingly discussed in the chapter on Nerves (Chapter IX.), as their laws of action upon muscle and nerve are similar. 3. *Chemical stimuli,* among which must be regarded in general all those substances which rapidly induce changes in the chemical constitution of the contents of the muscle-tubes. At the point of application they cause rigor as well as contraction. The majority of them act even when in a very diluted condition; especially is this the case (Kühne) with mineral acids (HCl in solutions of 0·1 per cent.), solutions of metallic salts, lactic acid, diluted glycerin, and ammonia even when present in traces in the atmosphere. To the list of chemical stimuli belongs also distilled water, especially when injected into the vessels of muscles. The greater number of these substances have no stimulating action upon the nerves (*e.g.* ammonia), or only when very concentrated. 4. *Thermal stimuli, i.e.* temperatures above 40° C., strongly heated bodies inducing contractions very readily on coming into contact with muscle. 5. Mechanical stimuli, *i.e.* some sudden and marked change of form occurring at any point, induced, for example, by pressure, torsion, tearing, extension, &c. The method of operation of these stimuli is as yet quite unknown.

The same intensity of stimulus does not always produce in the same muscle the same effects—it may liberate at different times dissimilar quantities of energy; that is to say, the irritability of a muscle is not always constant. It depends, as far as has yet been discovered, upon the following circumstances: 1. It is greatest in any organism under a certain medium tem-

perature, and diminishes as the temperature rises or falls above that mean. 2. It is diminished for a time by previous activity: this diminution is called ' *exhaustion* ' of the muscle, and it may owe its origin to the following circumstances: (*a.*) The accumulation in the muscle of certain products which are formed in quantity while the muscle is acting, and which are probably not absorbed with sufficient rapidity. These must be supposed to have some prejudicial influence upon activity—a supposition which has recently been confirmed (J. Ranke). The products are carbonic acid and the acid of the muscle, whether it be a free acid or form part of an acid salt. (*b.*) The deficiency of the special constituents upon the consumption of which muscular activity depends, and which cannot be remedied quickly enough during the active condition. In all probability both causes are concerned in the production of exhaustion. 3. In muscles which are removed from the body, or which are deprived of oxygen by ligaturing their arteries (Stenson), as well as in those of the dead body, irritability diminishes after a slight period of exaltation, but more quickly in warm- than in cold-blooded animals. The diminution in irritability occurs *pari passu* with the development of rigor, is accelerated by the same circumstances (p. 244), and has entirely disappeared by the time that rigor is complete. 4. All influences which essentially modify the normal composition of muscle-substance in the living body diminish and tend to destroy irritability. 5. If irritability has been much diminished by any of the above means except the last, and rigor has not yet occurred, it may in a certain sense be recovered by passing for a long time a strong and constant galvanic current through the muscle in the direction of its length (Heidenhain), the probable explanation of which will be given in Chapter IX. when speaking of the modifications of nervous irritability. 6. Another means of restoring irritability when it has been diminished by ligaturing the arteries supplying a muscle, is by renewing the circulation, which, however, only operates so long as rigor is incomplete.

As the majority of solutions, and even distilled water, have a stimulating and destructive action upon muscle, there are but few indifferent liquids in which it undergoes no change. Such are dilute solutions of $NaCl$ (0.6 per cent. being the most favourable, O. Nasse), or of other sodium salts, the per-centage strength which is most favourable being determined by the molecular weight of the salt (Nasse). Less favourable than these, but less

destructive than distilled water, are solutions of boracic acid (1·5–2 per cent.), and of arsenious acid (Brücke).

Exchanges of Matter of Muscle in a State of Activity.

The following chemical processes have been shown to occur in active muscle:

1. Carbonic acid is formed and given up to the blood, or in the case of excised muscles, to the air. This excretion of carbonic acid is considerably greater during states of activity than of rest. It occurs in excised muscles (Matteucci, Valentin) as well as in those of a living animal or in those through which a stream of blood is artificially maintained; in the latter case the venous blood yields more carbonic acid while the muscle is active than while it is at rest (Ludwig and Sczelkow, Ludwig and Schmidt). The whole body excretes more carbonic acid during periods of activity than when in repose (Regnault and Reiset, p. 156).

2. Muscles in the body, and muscles through which blood is artificially forced, consume more oxygen during activity than during rest, as is proved by the fact that venous blood contains less oxygen in the former case than in the latter (Ludwig and Sczelkow, Ludwig and Schmidt). The whole organism, also, requires more oxygen during exertion than at other times (Regnault and Reiset); but the difference is much less than that between the amounts of carbonic acid excreted under the same circumstances (Pettenkofer and Voit).

An increased consumption of oxygen in the case of excised muscles while in action cannot be detected by direct measurements (Hermann).

The absorption of oxygen is not immediately demanded for the purposes of contraction, as muscles are capable of continued exertion in a vacuum or in an atmosphere containing no oxygen. Muscles, moreover, contain no store of oxygen which is capable of removal by exposure to a vacuum (Hermann).

3. During a period of activity muscle becomes *acid* (du Bois-Reymond), just as in rigor; probably the acid is the same in both cases.

4. The composition of muscle alters during activity in such a manner that the constituents which are soluble in water

decrease in quantity, while those soluble in alcohol increase (Helmholtz).

The above are the only processes which are certainly known to take place in contracting muscle. Others have, in addition, been mentioned, some of which have been the result of faulty methods of observation, while others have been disproved, or rendered doubtful, by the occurrence of opposite results. The two chief methods of investigation employed are the following : 1. The comparison of the excreta of the organism during rest and exertion; from the list of substances excreted in greater quantity during exertion, conclusions may be drawn as to the substances used. 2. The comparison of the chemical composition of muscles (preferably of the same animal) after periods of repose and of continued exertion. In these experiments muscular exertion may be undergone either (*a*) by muscles in the living animal (as, *e.g.* by inducing the tetanic convulsions of strychnia-poisoning, one limb being kept at rest by the previous division of its nerves), or (*β*) by excised muscles.

There exists, however, in the second method of investigation a source of error which renders useless the majority of the experiments. It will appear from what is said hereafter that the chemical processes occurring during contraction and rigor are identical in nature; indeed, two similar, excised muscles, after having undergone rigor, have exactly the same composition (except as regards the amounts of carbonic acid excreted), whether one has previously been in a state of activity or not. As, now, the requirements of chemical analysis are almost always such as to induce immediate rigor in the muscles under experiment (they have to be at once 'scalded'), we cannot expect to find any difference in composition in the case (*β*) when excised muscles are used ; and if differences do appear, no certain meaning can be attached to them. In the case (*a*), on the other hand, where the exertion is undergone by the living animal, the blood-current continually removes the products of the material exchanges occurring during the periods of activity, in consequence of which the muscles which have been contracting contain, after rigor, less of those products than those which have been at rest. If, now, we regard as the products of activity those substances only which we can find in increased amount in the muscles which have been active, we shall commit an error (if the occurrence of rigor is not prevented) which will lead us to conclusions exactly the reverse of true. The following are the chief theories of the material exchanges occurring in active muscle :—

1. That muscles in contracting *consume* (*oxidize*) *albuminous bodies.* This theory rests upon (*a*) a supposed increase in the amount of urea excreted during muscular exertion, which, however, does not really occur (Voit); (*b*) a supposed diminution in the albumin contained in muscles during their activity (J. Ranke)—a diminution which, according to others (Nawrocki), is slight enough to be set down to the unavoidable errors of experiment apart from the consideration of the important error above mentioned; (*c*) a supposed accumulation in active muscles of nitrogenous products of oxidation, viz., of creatine (J. Liebig, Sorokin, Sczelkow—the presence of which was not confirmed by the researches of Nawrocki), hypoxanthine, etc.

(Scherer): such an accumulation appears to occur under certain circumstances, but not as the immediate result of muscular exertion.

2. *That muscles produce, during activity, grape sugar* (J. Ranke): the supposed increase is, however, so extremely slight (0·005 per cent.), that, apart from what has been said above, it cannot form the basis for any conclusions.

3. *That muscles produce, during activity, fats* (J. Ranke): this statement is useless as long as the intramuscular nerves, a great part of which is soluble in ether, are not excluded.

4. *That muscles during contraction* oxidize volatile fatty acids (Sczelkow): for the reasons before mentioned the experiments cannot be regarded as affording conclusive proof.

On the whole, therefore, we must reject Ranke's theories, based upon the data given above, that active muscle consumes albumin and forms creatine, sugar (lactic acid), fats and carbonic acid. In their stead the following may be stated as to the nature of the chemical processes of muscular contraction.

The chemical actions which take place during contraction and rigor of muscles are most probably identical (Hermann). This conclusion is drawn from the facts: 1. That an excised muscle yields the same amount of carbonic acid whether it enters at once into rigor or has previously generated carbonic acid by contraction: therefore, the more carbonic acid there is produced by contraction, the less does the muscle evolve on entering afterwards into rigor (Hermann), the original composition being supposed the same in all cases. 2. That the same relationship seems to exist in the case of the lactic acid—at least, a muscle which has been active in the body, on entering into rigor after excision, produces less acid than one which has remained at rest (J. Ranke). 3. That both the processes are independent of the absorption of oxygen, muscles being able to contract and to enter into rigor in a vacuum or an atmosphere of some indifferent gas. They are, therefore, processes not of oxidation, but of decomposition, in which stronger affinities are saturated or satisfied, and energy in consequence liberated, as was explained on p. 217. 4. That recovery is possible to muscles in states of exhaustion after continued activity, as well as in states of incomplete rigor, by means of the circulation of blood through them. 5. That muscles can pass immediately from a condition of activity into one of complete rigor (rigor of the second stage).

It is now only necessary, for the two processes of contraction and rigor to be exactly comparable, that there should occur

a separation of myosin in the gelatinous modification, in which,
as was said before, no change in optical appearance is effected.
Such a separation is rendered most probable by the circumstance,
just alluded to, that muscles may pass at once from a condition
of activity into one of complete rigor; for, as the second stage
in the coagulation of myosin of necessity implies the occurrence
of the first, it follows, in the case before us, that the first stage
must have occurred during activity.

The following may in all probability be regarded as the simplest theory
of the chemical processes occurring during contraction and rigor: Muscle
contains at any moment a store of a complicated nitrogenous substance dis-
solved in the contents of the muscle tubes and in the muscle-plasma,
which may be described, for the sake of brevity, as the 'energy-gene-
rating,' or 'inogene, substance.' This 'inogene substance' is capable of
undergoing a decomposition in which energy is evolved, and the following
products yielded, viz. carbonic acid, sarco-lactic acid, probably glycerin-
phosphoric acid (p. 245) and a gelatinous body, myosin, of an albuminous
nature, which separates spontaneously, and afterwards contracts firmly,
becoming probably concentrated. This decomposition occurs spontaneously,
but slowly, while the muscle is at rest, the rapidity of its occurrence being
determined by the height of the temperature. It takes place instantaneously
at the temperature of heat-rigor. It is, moreover, at once accelerated by
stimulation; and this acceleration is essentially what occurs during the
active condition. When the substance is entirely used up, muscular activity
is no longer possible.

The 'inogene substance' has not hitherto been isolated, as in every method
of chemical investigation yet devised the characteristic decomposition occurs.
The latter may, indeed, be prevented by subjecting the muscle suddenly to
a strong heat (scalding) or to the action of mineral acids, but both these
methods destroy the substance. As regards its composition, it would seem
to resemble hæmoglobin (p. 36), as both yield an albuminous body on de-
composition. On account of the analogy between the chemical processes of
muscular activity and of rigor we must suppose an expenditure of glycogen
(O. Nasse) to occur during the former as during the latter.

As the essential energy-yielding substance is used up during
muscular exertion, a continual renewal of it is necessary in
order that a muscle may retain its active properties. This is
effected, as already mentioned, both after contraction and rigor,
by the blood. The blood effects the recovery of the muscle,
not only by the production or renewal of the 'inogene sub-
stance,' but also by the removal of the products of decomposition
themselves which are harmful to the muscle. Blood removes
from muscle carbonic acid and, most probably, also sarco-lactic
acid (du Bois-Reymond), both deleterious substances; and it

gives up to that tissue oxygen.   It is, however, evident that oxygen alone cannot repair all the losses sustained by muscle, as carbon and hydrogen are continually leaving it in the form of carbonic and lactic acids.   The blood must, therefore, supply to it, besides oxygen, organic materials containing carbon and hydrogen.

The whole of the products of the decomposition of 'inogene substance' do not leave the muscle; for, as the excretion of nitrogenous material is not increased by muscular exertion, it must be concluded that the myosin remains within the muscle.   In consequence of this, and of the fact that it is not the prepared substance, but only the materials necessary to form it, which are conveyed to the muscle by the blood, it is most probable that the recovery of muscle after exhaustion, apart from the mere removal of the effete materials, consists in a synthesis of the 'inogene substance,' in which myosin plays a part, and for which the blood supplies oxygen and some non-nitrogenous organic body hitherto undiscovered (Hermann).   Myosin, therefore, according to this theory, undergoes in muscle a complete cycle of chemical changes.

The following conditions are necessary for the restoration of muscle: 1. The addition of oxygen, which may take place, though to a limited extent, in excised muscles.   2. The addition of the yet unknown organic body referred to above, of which it is possible that excised muscles may contain a slight store.   The latter supposition may at least be taken to explain the facts that restoration is, to a certain extent, possible by simple exposure to the air, and that irritability is retained for a longer time when the surrounding atmosphere contains oxygen.   3. The presence of myosin capable of being used, *i.e.* which has not passed into the firmly-contracted condition. A consideration of this third condition will explain why the restoration of muscular tissue by means of the circulation is limited.   The synthesis of the 'inogene substance' in which oxidation is one of the processes seems to be analogous to the synthesis of hæmoglobin, in which also oxygen plays a part (p. 180).

The chemical process, which forms the basis of muscular activity, and the process of restoration, occur without any essential dependence one upon the other: it follows, therefore, that the excretion of carbonic acid by the muscles and by the whole organism, which is characteristic of the former process, and the absorption of oxygen, muscular and general, which is an important feature in the latter, are equally independent (p. 157).   It must, however, not be forgotten, that whenever the decomposition of 'inogene substance' is accelerated, as during muscular activity, the processes of restoration and repair are also increased, *i.e.* that muscle takes up more oxygen from the blood during activity than during repose; for it is in

this way that the danger of exhaustion is diminished. This regulating action is explained chiefly by the fact that the circulation is accelerated in a muscle by its contraction (Ludwig and Sczelkow). If the exertion is excessive, the repair of the 'inogene substance' cannot keep pace with its expenditure, and the muscle becomes for the time acid, and can only be stimulated to contraction with difficulty. This condition is called exhaustion, and resembles the state of approaching rigor, such as is induced by subjecting muscle to heat.

Certain circumstances render it probable that individual fibres of a muscle may pass into a condition of complete rigor, especially if the previous exertion of the muscle have been excessive. In such cases the myosin is no longer capable of use in the synthetic process of restoration; and the loss thus occasioned must be repaired by the formation of 'inogene substance' in some other manner. There must therefore occur, in addition to the above-mentioned regular functional exchange of matter, another process which may be described as the material exchange due to wear and tear. We have only now to suppose that the myosin of the completely coagulated fibres decomposes further with the formation of creatine, the separation of which would serve to increase the amount of urea excreted; and perhaps also of fat, as fibres which have undergone fatty degeneration are found in every muscle. This theory would serve well to explain the statements of the occurrence of increased nitrogenous excretions, &c., after muscular activity. Under such circumstances other albuminous bodies resembling myosin, which are held stored up in the muscle, would be used instead of the latter in the synthesis of 'inogene substance.' Such albuminous components of muscle are those which coagulate between 40° and 60° C.

According to the theory which has just been propounded, only non-nitrogenous substances are really used up. This is supported by the observation that the excretion of urea is not increased by muscular exertion (Voit). Attempts have been made to reconcile this observation with the consumption of nitrogenous material; firstly, by the supposition that the consumption of material by muscle was not in general increased during activity, and that therefore the same amount of energy was liberated as when the muscle was at rest, but in another form (Voit); and, secondly, by the theory that the increase in the extent of the material exchanges produced by exertion was counteracted by a corresponding diminution immediately afterwards (J. Ranke). That neither explanation is correct is shown by the fact of the increase in the excretion of CO_2 both at the very time of muscular exertion, and during longer periods of work alternated with rest. Since it was first stated that non-nitrogenous substances only were used up during muscular exertion (M. Traube), it has been directly shown that the quantity of albuminous materials used up during the time of exertion, calculated from the urea excreted, is not sufficient, even when an excessive heat of com-

bustion is assigned, to account for the work done (expressed in heat-units) (Fick and Wislicenus, Frankland).

It has been sought to explain the circumstance that muscular tissue takes up oxygen without immediately utilising it in the formation of carbonic acid, by the hypothesis (M. Traube) that the gas is first taken up by a ferment, which retains it until the moment of contraction, when it gives it up to the non-nitrogenous substances to be oxidized. This view agrees essentially with the theory of muscular activity given above: the ferment is myosin, which does not, indeed, store up oxygen until the periods of activity return, but which unites with that gas and some non-nitrogenous complex body to form a compound which decomposes during contraction, and thus sets the myosin free to be used again in the same manner.

It has, further, been supposed, in order to account for the fact that the quantitative ratio between absorbed oxygen and excreted carbonic acid is different during exertion and during rest, that in the former condition other substances are oxidized in muscle than in the latter (Ludwig and Sczelkow). This supposition is unnecessary, owing to the independence, which was above referred to, of the processes in which, respectively, oxygen is used (synthesis of 'inogenc substance') and carbonic acid formed (decomposition of 'inogene substance').

Among the effects of muscular exertion upon the constitution of the excretions, it has been mentioned that the degree of acidity of the urine is increased during muscular exertion (Klupfel); but this is denied by others (Sawicki).

Changes in the Form of Contracting Muscles.

The chief and most manifest result of the evolution of energy in active muscle, and which may be especially described as the work done by muscle, takes the form of *mechanical work—movement.* This movement consists in an alteration in the form of the muscle, viz. a diminution in length, affecting the primitive fibres, and an increase in thickness. The alteration is effected with such energy as to overcome even considerable resistances opposed to it. In the majority of cases the resistances are opposed to the diminution in length, and consist of forces which tend to separate the extremities of the muscle; the most frequent example, and the one to which all others are referred, being that of a muscle fixed at one extremity and supporting a weight attached to it at the other. By contraction of the muscle the weight is raised, and the mechanical work thus accomplished is expressed by the product of the weight into the height through which it is raised.

The diminution in length and increase in thickness of a

muscle on contracting are connected with a diminution in volume—a species of condensation. This may be proved by suspending a muscle in a vessel, provided with a narrow, upright tube protruding through the cork, the whole of which is accurately filled with a fluid. When the muscle is stimulated to contraction the fluid sinks in the narrow tube (Erman, Valentin). Muscle when contracted is also less elastic, and therefore more extensible, than when at rest (Ed. Weber).

After each simple stimulation directly applied, a single and rapid alteration in form occurs in the muscle, and is called a *contraction*. The diminution in length does not take place immediately on the application of the stimulus, but is postponed for the space of about $\frac{1}{100}$th of a second, during which time the muscle is, to all appearance, still at rest: this is called the ' period of latent excitation ' (Helmholtz). At the end of that time active contraction commences, at first with increasing, but afterwards with diminishing rapidity, and continues until a maximum is attained. The contracting forces then cease gradually to act upon the muscle, which is thereupon extended by means of the attached weight, at first quickly, but afterwards more slowly, to its previous length. If the muscle is not acted on by any weight, not even its own (as, for example, when it rests upon a surface of mercury), it retains approximately the form it had at the instant of maximum contraction (Kühne); and, if the weight is but slight, it does not completely attain its original length (Hermann). If we imagine the upper extremity of a vertically suspended muscle to be fixed, and an upright plate to travel quickly and regularly in a horizontal direction in front of the lower, a curve would be described upon the plate during the contraction of the muscle, the abscissæ of which would represent the times, and the ordinates the degree of contraction. Such a curve presents the following points of interest : From the instant of stimulation it runs at first for some distance upon the abscissa-line (latent period—period of latent excitation); it then rises, being at first convex, but afterwards concave towards the abscissa-line, until it reaches a maximum, after which, if the weight have been sufficiently large, it gradually falls again to the abscissa-line (Helmholtz).

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The time occupied in the evolution of energy in a muscle after stimulation may be discovered in two ways (Helmholtz) :—

1. A muscle to which a slight weight is attached is allowed to contract freely, in which case the distance through which the attached weight is lifted increases and diminishes in the same ratio as the contracting force. The muscle is suspended vertically, and its lower extremity is attached to a lever provided with a pen arranged in such a manner as to mark, when the muscle contracts, upon a surface moving with uniform velocity in a horizontal direction in front of it. This moving surface is either in the form of a cylinder rotating evenly about a vertical axis, as in Helmholtz's myograph, or of a smooth plate fixed to the extremity of a long pendulum, as in that of Fick. A curve is in this manner produced, of which the abscissæ represent the time, and the ordinates the degree or extent of contraction. As the latent period occupies an appreciable portion of the line traced by these means, the instant of stimulation must be indicated on the recording surface by some mark. This is most easily done by causing the moving surface itself in passing some point in its course to effect the stimulation, say by closing a current.

2. Contraction is not allowed to occur, but is hindered by means of weights placed in a scale-pan attached to the lever *dc* (Fig. 5),
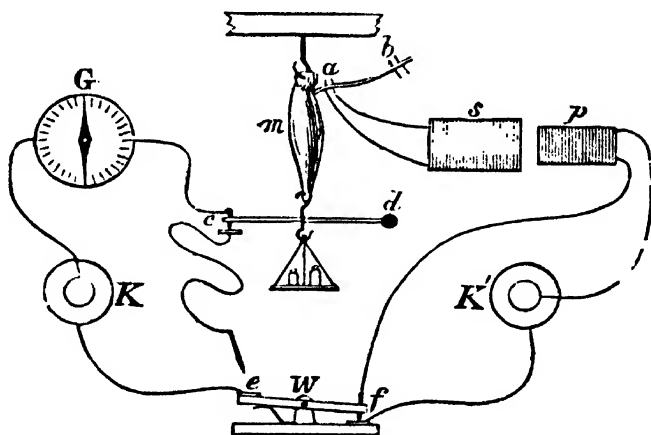
Fig. 5.

which is supported in such a manner that the weight cannot act upon the muscle while it is at rest, but only when it tends to contract. Each weight placed in the scale-pan ('*overload*') keeps the muscle in the position it occupies when at rest, until the contracting force (energy) attains an intensity equal to that of the *overload*. As the contracting force is evolved gradually after stimulation, the time intervening between stimulation and the lifting of the weight from its support, *i.e.* the breaking of contact at *c*, is greater the heavier the weight. If the muscle is not overloaded, the time from the application of the stimulus to the raising of the lever corresponds to the latent period. A degree of overloading is at last attained, which prevents any movement of the lever by the muscle, and therefore represents the limit to the evolution of the contracting

force. The measurement of the time from the moment of stimulation to the raising of the weight (*i.e.* to the breaking of contact at *c*) is effected by the method of Pouillet, according to which it is registered by the deflection of the needle of a galvanometer G, the current of which is made at the instant of stimulation, and broken at *c* when the weight is raised. The coincidence of closure of the galvanometer-current and the stimulation of the muscle is accomplished by pressing the point of the wire against the plate *e* of the commutator w, whereby the current from the battery K is closed, while that from the battery K' connected with the primary coil *p* is broken at *f*, in consequence of which an opening induction shock is transmitted by the wires from the secondary coil *s* to the muscle.

If the times registered by the above method be taken as abscissæ, and the corresponding weights as ordinates, a curve representing energy is obtained, which agrees with the ascending portion of the ordinary muscular curve, got by means of the myograph. The latter, however, deviates slightly from the former, on account of the weight suspended to the muscle in myograph-experiments in order to keep it extended (Klünder). The curve representing energy may also, by proper arrangements, be obtained directly (Fick).

Instead of making use of the shortening of muscle for the production of a curve, the thickening which it undergoes on contraction may, by a suitable apparatus, be registered in the form of a curve, which, as might be expected, agrees with that produced in the above manner (Aeby, Marcy). This method is applicable to the muscles of a living man.

Certain muscles have the characteristic that their contraction proceeds very slowly, and, in consequence, gives rise to a very extended muscle-curve : such, for example, are the muscles of the tortoise and of the heart (Marey), the latter forming the transition in rapidity of contraction between striped and unstriped muscles (see below). Cold, exhaustion, &c., hinder the progress of contraction (Valentin, Klünder) and diminish its extent (Volkmann).

The greatest degree of force which a muscle is capable of exerting, as measured by the weight which is just able to keep the muscle extended in the position of rest, as described in the second of the above experiments, is called the 'absolute power' of the muscle. . If an unweighted muscle be allowed to contract, and in the midst of contraction brought to a standstill suddenly by means of a weight, it will be found that a smaller weight is required to effect this according to the extent to which contraction of the muscle has already gone. The force of a muscle, therefore, diminishes during contraction, and is equal to nothing at the end of it. In order to show this, the weighted lever is so arranged by placing it nearer to the fixed extremity of the muscle, that a certain extent of contraction must have taken place before the muscle begins to act upon it (Schwann).

If two stimuli follow one upon the other so quickly that

the contraction induced by the first, although it has got past the latent period, has not reached its maximum before the second commences to operate, their united result is to produce a stronger contraction. That is to say, the second stimulus operates just as if the contracted form which the muscle had when it began to act were the natural form of the muscle (Helmholtz). From this it is evident that the maximum of contraction under the most favourable circumstances may be doubled, viz. when the difference in time between the two stimulations equals the duration of a single contraction from its commencement to its maximum.

Further, if a series of stimulations are brought to bear upon a muscle at very short intervals of time, no opportunity is afforded to the muscle of regaining its normal extension between any two of them; and, in consequence, it retains its contracted form during the whole series: this condition is called 'tetanus.' All continued muscular contraction, of which the body presents so many examples, must be regarded as tetanic, *i.e.* as being produced by a series of stimuli following closely one upon another (Ed. Weber). That such continued contraction is to be looked upon as the result of a series of single contractions, appears evident; firstly, because of the phenomenon of 'secondary tetanus,' to be described afterwards (du Bois-Reymond); and, secondly, from the evolution of the 'muscular murmur.' The latter may be heard by applying the ear or stethoscope to the tetanised muscle of a man (*e.g.* one that is kept under voluntary contraction); it appears to be a weak murmur in which a distinct note predominates—the muscular murmur or note (Wollaston). The vibrations of this muscular murmur, when the muscle is tetanised by an induction current, correspond per second with the number of stimuli applied (Helmholtz). As voluntarily tetanised muscles generally emit a distinct sound (of 19·5 vibrations per second), the number of stimuli proceeding from the motor central nervous organs during tetanus by the will must be 19·5 per second (Helmholtz).

If stimuli of a certain strength follow one another very quickly (*e.g.* if more than from 224 to 360 occur per sec.), no tetanus results (Harless, Heidenhain), and only the first produces a contraction (initial contraction, Bernstein). If the strength of the stimuli be increased, tetanus follows.

The best means of tetanising muscle is by using as stimuli a series of frequent electric shocks; such a series, for instance, as is produced by the continual opening and closing of an electric current. In order to study those characters of active muscle for the development of which a single contraction is too fleeting, *e.g.*, the chemical changes during activity, the evolution of heat, the negative variation of the muscle current, which the galvanometer, on account of the inertia of the needle, does not show in the case of a single contraction, it is best to tetanise the muscle experimented upon.

The first sound of the heart is most probably an instance of a muscular murmur of the usual pitch (Natanson, Haughton, p. 60); ventricular systole must therefore be a tetanic contraction. The muscular murmur may be heard, preferably at night, by stopping the ears with wax, and contracting the muscles of mastication. The depth of the muscular note was formerly given at from 36-40 vibrations per second (Natanson, Haughton, Helmholtz). When it became possible to determine it more exactly by the method given below, it was fixed at 19 vibrations per second —the audible tone is therefore the first harmonic of the primary note in the muscular sound (Helmholtz). The dependence of the note upon the number of stimuli applied per second becomes evident to any one who tetanises his own masseter muscle by means of an induction apparatus, the coils of which are placed in a distant room, the note being the same as that emitted by the interrupter of the machine used (Helmholtz). The fact that a muscle when tetanised by stimuli proceeding from the central nervous organs has a tone with an independent and characteristic number of vibrations was first noticed in the case of an animal, the muscles of which were thrown into tetanus by stimulating the spinal cord, and which then emitted the deep murmur of contracting muscle (du Bois-Reymond). In such a case the note is independent of that caused by the vibrations of the interrupter of the apparatus used. The muscular murmur may also be heard by fixing a frog-muscle, properly weighted, to one end of a short staff, the other end of which is inserted into the ear, and tetanising it by means of electricity. The vibrations may be rendered visible by imparting them, by resonance, to a strip of flexible metal or paper (Helmholtz).

If a muscle or a muscular fibre be stimulated to contraction at any one point, the remainder takes up and continues the condition of activity (Kühne). The rapidity with which the contraction is propagated along the muscle is equal to about 0·8 — 1·2 metres per second (Aeby, von Bezold), or, according to recent statements, probably a little more (3 metres, Bernstein); and it decreases with the temperature. Under the microscope contraction passes like a wave over the fluid contents of the muscle-tubes (Kühne); the transverse striæ approximate each other (Ed. Weber), and become smaller, while the doubly-refractive sarcous elements diminish in the direction

of their long axes (Brücke). The curved or zigzag position of the fibres while at rest (p. 243) disappears during activity (Ed. Weber). If the muscular fibres have lost their irritability, as, for example, through exhaustion, stimulation produces only local contraction, and puffy protuberances (Kühne) are formed, especially with powerful mechanical stimuli, by the local contraction and thickening. These were formerly called ' idio-muscular contractions,' a name which can on theoretical grounds no longer be retained (Schiff).

On powerful local stimulations of a mechanical nature these puffy appearances may occur, even in muscles which are perfectly irritable, together with the general but weaker contraction of the whole length of the fibre. This may result, for example, from a powerful blow on the muscles of the upper arm.

In accordance with the recent statements concerning the minute structure of striated muscles, numerous theories have been devised respecting the alterations which take place on contraction ; but they are too diverse to be inserted here.

On the Amount of Work done by the Contracting Muscle.

1. WHEN THE TRANSFORMATION OF ENERGY WITHIN THE MUSCLE IS AT ITS MAXIMUM.

In the first place the most simple case will be considered, that, namely, in which, by as powerful an irritation as possible, as much energy becomes kinetic within the muscle as it is capable of yielding.

An idea may be formed of the mechanical changes which occur in a muscle when it contracts (Ed. Weber) if we imagine that, under the influence of an excitant, and in consequence of the chemical processes which result from its action, the muscle AB (Fig. 6) suddenly assumes a new natural form Ab, which differs from the first in being *shorter*, *thicker*, and *less elastic* (p. 256), and which tends to return to its original shape. When the muscle passes from the first into the second, or contracted, form, it behaves exactly as if it had been stretched beyond its natural length, and in virtue of its *elasticity* had tended to assume the new form. The same happens if the muscle when at rest be extended by a weight, only that in this case the length attained is greater than if the same muscle were stretched while contracted. The difference between these two lengths is, of course, the height through which the weight is

lifted (*Hubhöhe*), which, for the sake of brevity, we may term the *lift*. The product of the weight raised into the height through which it is raised, *i.e.* the product of *load* into *lift*, expresses the work done by the muscle.

A moment's consideration, assisted by a glance at Fig. 6, serves to show that when the extensibility of the contracted muscle becomes considerably greater than that of the muscle at rest, the lift of the muscle will diminish as the load increases, being with a certain load nothing, and finally becoming negative. That is to say, when the load attains a certain amount, it will no longer be raised on the application of a stimulus to the muscle; and also, as it increases still more, stimulation will

Fig. 6.
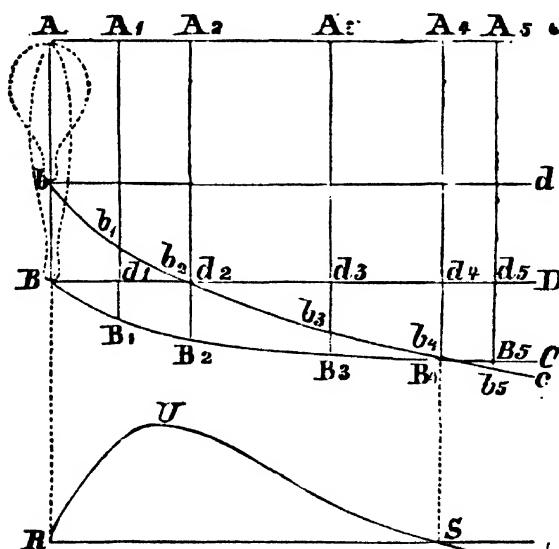
cause *elongation* of the muscle, instead of *contraction*. Let AB, in Fig. 6, be the natural length of the uncontracted muscle; moreover, suppose loads of various sizes to form abscissæ on the axis BD, and the extensions corresponding to them to be carried down as ordinates; then BC is the curve of extension of resting muscle, and A_1B_1, A_2B_2, A_3B_3, etc., are the lengths of the muscle corresponding to the loads Bd_1, Bd_2, Bd_3, etc. Again, let *Ab* be the natural length of the *contracted* muscle (for a given stimulus); as, now, its elasticity is to a certain extent less than that of the muscle at rest, the curve of extension, *bc*, obtained in the above manner, will fall more

abruptly than BC, and cut it in a point B_4. As A_1b_1, A_2b_2, A_3b_3, A_4b_4, etc., are the lengths of the *contracted* muscle under the different loads, the lines B_1b_1, B_2b_2, etc., between BC and bc, are the lifts of the muscle on stimulation. It is seen at once that they become smaller and smaller, being at $B_4 = 0$, and after that point (B_5b_5) negative. That is to say, elongation takes the place of contraction on the application of a stimulus, A_5B_5 extending to A_5b_5. The work done by the muscle when carrying the various loads is found by multiplying the abscissæ (Bd_1, Bd_2, etc.) into the corresponding lifts. It is at once seen that this product $= 0$ at two points, viz., at B and at B_4; that it is greatest a little before the middle position between those two points is reached; and that, on the other side of B_4, it is a negative quantity. The variations in the work done may be represented by the curve RUS.

Many facts agree with this view, as, for instance, the easily observed diminution of the height through which a weight is lifted as the weight increases, the elongation of the muscle when made to contract whilst bearing very heavy loads (Weber),[1] and some other phenomena to be afterwards mentioned.

The relations of muscles of the same kind (from the same animal), but of different size, are very simple. The activity of contraction being at its maximum, the weight which a muscle can lift to a given height will increase as its transverse section becomes larger, and, the weight being constant, it will be lifted higher the longer the muscle. The demonstration of this is easy. Let us imagine n similar muscles to be suspended close together in parallel lines; suppose each of the muscles to have attached to its free extremity a unit-weight, which it is capable of raising to a unit-height; a muscular system is thus arranged which has n times the extent of transverse section of one muscle, and which can raise n units of weight through a unit of height. On the other hand, if the n muscles be connected together end to end, and the system suspended by one extremity while a unit-weight is attached to the other, a muscular arrangement is produced which is n times as long as in the preceding case, and which can raise a unit-weight through n units of height.

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[1] According to Fick, no amount of weighting produces elongation during contraction (or '*negative*' *Hubhöhe*): he supposes therefore that the two curves bc and BC do not cut, but are asymptotes one to the other.

We may render these laws evident by diagrams similar to the one represented in Fig. 6 , if we hold in view the fact that the extensibility of a muscle is directly proportional to its length and inversely proportional to its cross section.

The amount of work which is done under the influence of the most powerful excitant would appear to be the natural measure of the maximum amount of energy which can become kinetic in a muscle, when its irritability is greatest. The amount of work done is, however, very variable. It depends, for example, upon the weight, as was shown above. Moreover, it follows from Weber's theory, that it is greater if the load be continually diminished as it is being raised (Fick) ; and, as a fact, many muscles in the body act on levers in such a manner that the moment of the load about the point of support diminishes as contraction proceeds. The maximum amount of work which 1 grm. of frog's muscle can perform varies between 3324 and 5760 grammeters (Fick).

Commonly the functional activity of a muscle is determined by ascertaining the maximum power of shortening which it displays on the application of the strongest excitation. The magnitude of this so-called ' absolute muscular force ' expressed in units of weight, is dependent upon the area of its cross section, and is therefore expressed in relation to the unit-area of the section. A square centimeter of frog muscle corresponds to between 2800 and 3000 grammes (Rosenthal), and a square centimeter of human muscle to between 6000 and 8000 grms. (Henke and Knorz, Koster).

In a muscle separated from the body, the so-called 'absolute force' is determined by the method of 'overloading' which has been described at p. 258. Other methods depend upon the fact that the weight which represents this absolute muscular force is, according to Weber's theory, the same as would be capable of stretching the unloaded and contracted muscle to the length occupied by it when unloaded and at rest (*i.e.*, in Fig. 6, the weight corresponding to the abscissa Bd_2) ; and, in addition, the same as would be necessary for loading the muscle in order that, on contraction, it should regain the length it occupies when uncontracted and not loaded. The determination of this force in man is effected amongst others in the following ways (Weber):—When we stand on tiptoe, or, more correctly, when we rest our weight on the heads of the metatarsal bones, the gastrocnemii muscles, through their insertion into the os calcis, exert an action upon a lever of the second kind, the fulcrum of which is situated at the point of junction of the metatarsal bones to the ground ; the weight (of the body)

acts upon the point of the foot, through which the line of direction of the centre of gravity passes. If the body be now laden with weights until it is impossible to raise the heel from the ground, then the absolute force of the gastrocnemii is equal to the moment of the weight (body + weights) into its arm, divided by the length of the arm acted upon by the muscles; this value, when found, has only to be reduced in terms of the cross section. The mean cross section of a muscle is determined by dividing its volume (which is equal to its absolute weight divided by its specific weight) by its length.

The method of Schwann (p. 259) measures as it were the absolute force of a muscle in the different conditions of its shortening, when possessing the different lengths between $A\,B$ and $A\,b$ (Fig. 6) : as, however, in the case of the length $A_1 b_1$, the force found is equal to the weight which can stretch the active muscle $A\,b$ to the length $A_1\,b_1$, it is represented by the abscissa $B\,d_1$. Schwann's experiments afford a means of determining the curve which represents the extensibility of active (*i.e.* contracted) muscle, at least of the portion $b\,b_2$ (Hermann).

In the condition of muscular fatigue (p. 249) the absolute force of a muscle diminishes, as well as its power of shortening. When the stimulus is at its maximum, and the load borne by the muscle remains constant, the lift diminishes by an equal amount with every successive muscular contraction, providing that the time which intervenes between successive contractions is always the same. The longer the interval between successive stimulations, the smaller the diminution in the lift. The influence of the time which intervenes between ·the contractions is most marked when the muscle is in a state of fatigue. The times between the contractions remaining constant, the differences in the contractions become less perceptible as, soon as the muscle no longer contracts so as to have the length which it possessed when at rest and unweighted; the curve which represents the magnitude of the muscular contractions, which up to this point is rectilinear, now becomes a hyperbola, which is asymptotical to the curve which indicates the extensibility of the uncontracted muscle.

During tetanus a muscle executes no external mechanical work, as no weight is lifted by it; the weight already lifted to a certain height being merely maintained at that height. As the chemical changes which go on in a muscle which is in a state of tetanus are greater in amount than in a muscle at rest, we must assume that a tetanised muscle actually does perform work, the muscle losing and immediately thereafter regaining the whole of its tension during the extremely short interval between two successive stimulations ; this sudden regain of tension must, whenever it occurs, lead to a development of heat. One must seek for the equivalent of the tissue-changes which go on in the tetanised muscle, in the heat which is generated. The continually recurring changes in the tension of a muscle are

probably the cause of the ' *bruit musculaire,*' or muscular noise, to which reference was previously made. It has not hitherto been possible, even with the help of the most delicate arrangements, to demonstrate that at the time of the production of the muscular noise the load borne by a muscle is slightly lifted up and down.

2. WHEN THE ACTIVITY OF THE MUSCLE IS NOT AT ITS MAXIMUM.

The lift and the work done by a muscle, when the stimulus applied to it is constant, but of moderate intensity, appear to follow the same laws as hold in the case of the muscle excited by an intense stimulus.

If the strength of the stimulus varies, the degree of muscular activity varies also ; the new form which the muscle tends to assume, under the influence of the stimulus, differs, both in elasticity and in length, less from that which the muscle possessed when at rest, the weaker the stimulus. It has not yet been determined according to what law the strength of the stimulus affects the intensity of the active condition of a muscle. It is asserted that as the strength of the stimulus increases the active condition increases, although not with the same rapidity (Hermann) ; but it is also asserted that the active condition increases at equal rate from 0 up to a certain point, but that after a certain strength of stimulus has been attained it remains constant (A. Fick).

The methods which are adopted in making such determinations are the following :

1. The strength of the stimulus is determined which must be applied to the muscle in order that it should perform a definite task, such as the slightest possible movement of an excessive load (p. 258).

2. The load remaining constant, the lift is determined for stimuli of varying strengths (Fick).

If the changes in the elasticity of the muscle which correspond with every change in its form were known, one might, as in Fig. 6, construct, for every case, the extension curve of the active muscle, and so determine the height to which a weight would be lifted for every weight and for every degree of muscular activity. The relation between changes in elasticity and in form is, however, unknown, and determinations of the height to which

a known load is lifted permit of no conclusion being arrived at as to the natural form of the *unloaded* muscle (for the same degree of activity). Although the extension curves of the contracted muscle cannot be constructed *à priori*, yet Fig. 6 shows us that the line *bc* approaches more closely to BC and is proportionately less inclined to BC the smaller the activity of the muscle, and the weaker the stimulus. Hence the differences between the heights to which different weights are lifted must diminish as the strength of the stimulus diminishes, and the weakest stimulus capable of exerting an action must therefore lift to a slight extent as well the smallest as the heaviest weight—in other words, in order to produce the minimum lifting of 1 gramme or 100 grammes, the same strength of stimulus is required; experiment confirms this conclusion (Hermann).

From what has been stated it follows that a certain stimulus leads to the performance of very varying amounts of work in muscles which are differently weighted : this is explained by the supposition that the effect of weighting a muscle is to convert it into a new body, possessed of more potential energy than before.

The influence of the weight borne by the muscle must be even greater than the preceding statement implies, as it exerts an influence on the material exchanges which go on in the muscle.

Even in the case of the shortening which occurs during *rigor* (p. 244), the heights to which different weights are lifted, and the *absolute muscular power*, may be determined. These heights are, in the case of light weights, greater, in the case of heavy weights smaller, than when the living muscle is excited by the strongest possible stimulus : the natural form of the muscle in a state of rigor is therefore, according to Weber's theory, shorter, but its extensibility is greater, than that of the active (contracted) muscle ; the absolute muscular power is, in the case of the rigid muscle, smaller than in that of the contracted muscle (Walker).

d. Thermic and Electrical Phenomena of Muscle.

Thermic Phenomena.

Muscles removed from the body, as well as muscles which retain their connection with it, are hotter during *contraction* (Helmholtz, Béclard) and during *rigor* (v. Walther, Huppert, Fick and Dybkowsky, Schiffer) than when in a state

of rest. Both conditions lead, therefore, to a development of heat—in other words, the generation of heat which goes on in the muscle which is inactive, increases when it becomes active, or passes into a state of rigor.

The production of heat which is observed in rigor occurs simultaneously with the shortening of the muscle (Fick and Dybkowsky).

That heat is developed in muscle during contraction was formerly only proved in the case of tetanus; lately, however, it has been shown even in the case of individual muscular contractions (Heidenhain).

The determination is made by placing one thermo-electric junction, or one series of such junctions, in contact with the muscle, which is made to contract, whilst another junction or series of junctions is maintained at a constant temperature. (This is most easily effected by placing the second junctions in contact with a second corresponding muscle, which is kept at rest.) In the earlier experiments, needle-shaped thermo-elements were employed, which were either thrust into or passed through the muscle experimented upon, so that the junction was in contact with the muscular substance. In the more recent researches, thermo-piles, composed of a combination of many bismuth and antimony junctions, have been employed, one set of junctions being placed closely in contact with the muscle (Heidenhain).

In frog muscles the heat generated during individual muscular contractions amounts to between $0°\cdot001$–$0°\cdot005$ C.: during tetanus it may be as great as $0°\cdot15$ C. It is yet unknown at what state of a muscular contraction the development of heat occurs.

The heat developed during rigor is likewise ascertained by thermo-electric methods; one set of junctions being maintained at a constant temperature (Schiffer). Another method consists in placing the bulbs of two similar mercurial thermometers into two muscles, of which the one is yet living, the other is in a state of rigor. These muscles are dipped in an indifferent fluid, which is then warmed: when the temperature which produces heat-rigor is attained, the thermometer which was placed in the yet living muscle indicates a sudden rise in temperature (Fick and Dybkowsky). That heat is developed during *rigor mortis* is proved, in the case of the uninjured dead body, by the fact that after death the body takes a longer time to cool than the body which is artificially heated after cadaveric rigidity has set in (Huppert). The development of heat during rigor mortis explains post-mortem rises in temperature; and indeed the occurrence of the latter (in certain cases) first led to the supposition that an evolution of heat is associated with rigor (Walther).

Even when a muscle is stretched, a very slight evolution of heat occurs (Schmulewitsch, Westermann).

Concerning the proximate causes of these evolutions of heat we possess mere assumptions, which will be noticed in the sequel.

Electrical Phenomena.

If a muscle be cut so as to present a transverse section, and if the two ends of a galvanoscopic circuit, especially one which contains a delicate multiplier or mirror-galvanometer, be applied to a muscle in such a manner that one end is in contact with the transverse section and the other with a point of the longitudinal surface, the galvanometer will indicate the existence of a current (Nobili, Matteucci, du Bois-Reymond). This current passes through the galvanometer in a direction from the longitudinal to the transverse section, and therefore, in the muscle, in a direction from the transverse to the longitudinal section. This, which is called the *muscle-current*, is also obtained if any strip of muscular tissue, however small, obtained by longitudinal division of a muscle, be substituted for the whole muscle in the above experiment, provided that the strip is bounded by a transverse section to which one electrode of the galvanometer is applied, and that the other electrode is applied to the longitudinal surface ('*artificial longitudinal section*'). In this case the artificial longitudinal section bears the same relation to the transverse section as did the natural longitudinal surface ('*natural longitudinal section*') in the former case. It seems evident that an individual muscular fibre would also exhibit a muscle-current.

If a living muscle or a bundle of muscular fibres be taken, and the vitality of the tissue be destroyed over a limited length of the muscle or muscular bundle by caustics, by crushing, or by the application of heat, the muscle or muscular bundle will be divided into living portions, which are separated from one another by a dead portion, which is inserted between the former as an indifferent conductor of electricity might be. In this case every point in the cross line of demarcation between the living and dead muscle, and in general every point in the area of dead muscle, behaves, in reference to the longitudinal surface, as the cross section in the experiments previously alluded to. If such an artificial limitation of the living muscular fibres be also called an *artificial cross section*, we may state that generally, in whatever way it is made, *the artificial cross section of a muscle is negative in respect to the natural or*

artificial longitudinal section. The nearer the two poles of the galvanometer are to the centre of the longitudinal and cross sections respectively, the greater the intensity of the current which it indicates.

Amongst the many necessary precautions which must be taken in conducting these researches, we can only mention here that the animal tissues which are the subject of experiment must not be brought directly into contact with the metallic ends of the galvanometer, or of the wires connected with these ; for it is well known that two apparently perfectly similar pieces of metal (*e.g.* two copper wires) when brought into contact with a moist conductor—and all the animal tissues may be considered as such— form a galvanic chain, the current of which must cause a deviation of the needle of the galvanometer.

Pieces of zinc which have been amalgamated do not, however, give rise to a current when they are connected by means of a solution of zinc sulphate ; the two pieces of metal behave under these circumstances as if they were ' absolutely similar.' Relying upon this property, the two poles of the galvanometer are connected (in all researches in animal electricity) with two amalgamated pieces of zinc; each of these pieces dips into a vessel containing solution of sulphate of zinc, and from each of these vessels there projects a pad of filtering paper soaked with the same solution. The animal tissue the electro-motive properties of which are to be investigated is now so arranged that it completes the circuit between the two pads, bridging over from one to the other.

The animal structure is protected from the injurious effect which the solution of zinc sulphate would exert upon it by the interposition of an innocuous conductor; this consists of sculptor's clay which, having been dried, is made into a paste of suitable consistence by means of a 1 per cent. solution of common salt.

The employment of these zinc electrodes possesses the additional advantage of preventing the return of the needle after its first deviation, which, if any other method were adopted, would occur in consequence of the *polarization* of the electrodes. Electrodes made of amalgamated zinc plunged into solutions of zinc sulphate are *non-polarizable.*

The muscular current may be demonstrated by methods other than the galvanometric. (1.) By the electro-chemical method, viz. by causing the muscular current to decompose a mixture of iodide of potassium and starch paste ; in this case iodine separates at the positive pole and colours the starch blue. (2.) The muscular current may be employed to stimulate nerves, as *e.g.* to stimulate the very nerve supplying the muscle ('physiological rheoscope '). In this case it is necessary, as is mentioned in Chapter IX., to allow the current suddenly to break into the nerves. This is effected by suddenly completing a circuit, in the course of which is the nerve of a prepared frog's leg, by interposing the longitudinal and transverse sections of a muscle ; at the moment of closure of the circuit, a contraction of the leg takes place.

When experimenting with a single muscle the arrangement is as follows.

The nerve belonging to the muscle (which we must imagine to be in contact with the natural longitudinal sections of all the muscular fibres) is suddenly allowed to fall upon the cross section of the muscle; a muscular contraction ensues. (These contractions, without the interposition of metals, were known before the muscular current was discovered.)

Not only are currents observed when the longitudinal and cross sections of a muscle are connected, but also when the electrodes are made to touch two points of one and the same section. A circle embracing a muscle and dividing it into two halves may be called the *equator* of the muscle. Now if in any longitudinal section, natural or artificial, two points be taken for investigation, of which one lies nearer to the equator than the other, it will be found that the former is positive in relation to the latter (which is nearer to the cross section). Similarly, if any two points of a cross section of a muscle be investigated, which are unequally distant from the axis, it will be found that the point which is near the axis is negative in reference to the point which is further away from it (and which therefore is nearer the longitudinal surface).

No currents are observed when the electrodes touch two points which are equidistant from the equator of a longitudinal section, or two points equidistant from the axis of a cross section.

All these laws apply not merely to points on the same cross section, but also to points on different cross sections, and similarly to points on different longitudinal sections. Naturally, the two terminal points of the axis, and any two points on the equator of a muscle, when connected, do not cause a deflection of the galvanometer.

The currents which are obtained by connecting any two points on a longitudinal section, or any two points on a transverse section, are always very much weaker than those obtained when a point on a longitudinal is connected with a point on a transverse section, and they increase in strength as the difference in the position of the electrodes, in reference to the equator and axis, increases. The currents obtained by connecting two points on the same section are termed *weak currents*, as distinguished from the *strong currents* which pass between a longitudinal and transverse section.

In Fig. 7 the rectangular figure represents a piece of muscle: L L are its longitudinal surfaces, Q Q its cross sections, *a b* its equator. The thin lines

FIG. 7.
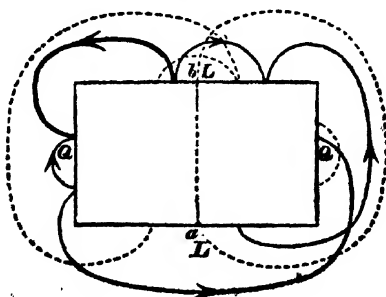
show combinations of points (on the same kind of surface) which give rise to weak currents; the thick lines illustrate the production of strong cur-

rents; the dotted lines show how different parts of a muscle may be arranged in reference to the electrodes, so as to exhibit no electric current.

If an oblique section be made through a muscle, or a vertical section be so altered by pulling as to furnish such a section, a departure is observed from the previously mentioned behaviour, inasmuch as the most negative point of the oblique section does not lie in the middle of it, but is in proximity to its sharp edge; similarly, the most positive points on the longitudinal section do not lie any longer in the equator, but nearer to the blunt edge of the section. In such a *muscular rhomb* a point in proximity to the latter is positive in relation to a point near the former, in spite of the two points being equally distant from the middle. In rhombic pieces of muscle currents must therefore pass from the acute to the obtuse edges which are super-added to the usual muscular current. Such currents are denominated *currents of inclination.*

All the phenomena which have yet been referred to may be explained by the law, that each individual muscular fibre exhibits the same (electrical) relations as the entire muscle, viz. that a transverse section through any part of it whatever is negative in relation to the longitudinal surface or section. By this hypothesis the 'strong' currents between the longitudinal and cross sections are explicable. The 'weak' currents are explicable simply by the hypothesis that when a portion of muscle presents cut surfaces, the latter rapidly die down to a certain depth, and are converted by this process of death into indifferent conductors; in this indifferent layer, the muscular current adjusts itself partly, and the electrical tension is not so distributed on the surface that the greatest positive tension is in the middle (equator) of the longitudinal section, the greatest negative tension in the middle of the cross section. The phenomena which were described at p. 272 are explained by the fact that a point possessing weak positive tension behaves negatively towards a point of stronger positive tension, and similarly a weakly negative point is positive in relation to a more intensely negative point; lastly, two points which possess the same amount and the same kind of electrical tension do not, when connected, give a current. In an oblique section the successively projecting active cross sections of the muscular fibres form a kind of battery, whose positive pole is near the obtuse, and whose negative pole is near the acute, edges: the current which is formed in this battery adds itself algebraically to the ordinary muscular current. In this way may be explained the phenomena of the 'currents of inclination.'

The electro-motive force of the current between the longitudinal and transverse sections of a muscle amounts, in the case of a frog, to as much as 0·08 of a Daniell; the electro-motive force of 'currents of inclination' may exceed 0·1 of a Daniell (du Bois-Reymond). All circumstances which produce muscular exhaustion diminish the intensity of the muscular current (Roeber).

In uninjured muscles separated from the body, currents pass from different points on the surfaces, which are of varying intensity and direction. Frequently tendons, *i.e.*, the indifferent conductors which are applied to the natural terminations

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of the muscular fibres, are negative in relation to the longitudinal section of the former, yet not so powerfully negative as an artificial cross section.

In frogs which have been thrown into a kind of hybernating state by the action of cold, the tendons are frequently electrically neutral, or positive in relation to the longitudinal section of muscle (du Bois-Reymond). *In a perfectly uninjured, unskinned animal, the muscles which are in a state of rest are entirely free from electrical currents* (Hermann); the currents originate during the preparation of the muscle, in consequence of injurious influences acting upon their surfaces. In frogs, for instance, amongst other such influences, is to be mentioned the action of traces of the caustic secretion of the skin.

The more these injurious influences are avoided, the greater the freedom of the muscle from electrical currents. In muscles which are at rest there are, therefore, no currents except those which are brought about by the negative electric tension of the artificial cross section in reference to the longitudinal section (Hermann).

In order to investigate the electrical currents of the muscles of unskinned frogs it is not sufficient to bring the electrodes, which are connected with the galvanometer, in contact with two points on the surface of the skin, as the skin at any point perpendicular to its surface, from without inwards, possesses electro-motive properties (du Bois-Reymond). These *cutaneous currents*, which are rapidly destroyed by the action of caustic alkalies, must be first eliminated (du Bois-Reymond). If this be done in such a way as to obviate the downward passage of the caustic to the muscle, at any rate up to the time when the experiment is made, the muscles are found to be entirely free from electrical currents (Hermann). Injuries which affect the whole muscular surface always cause the tendons to become negative in relation to the longitudinal surface of the muscle connected with them, for the fibres of the muscle die throughout their whole length, and therefore possess no current of their own, whilst under the tendon are placed the artificial transverse sections of many yet living muscular fibres; this is especially the case when the tendons present merely a thin aponeurotic membrane (as in the case of the gastrocnemius). The different deportment of the muscles of hybernating animals is most probably to be explained by a certain indifference which they present to slight transient injuries, which entirely agrees with their well-known sluggishness when stimulated.

When electrodes are placed in contact with two points on the surface of the limbs of skinned animals, or on two points of the surface of the body generally, currents are observed which are the resultants of the numerous individual muscular currents.

Muscles, or muscular fibres, which are entirely rigid, or which have been killed without rigor mortis occurring, exhibit no muscular current.

When a piece of muscle which is limited by a longitudinal and cross section is heated to a temperature which does not exceed that required to bring on *heat rigor*, the strength of the muscular current is increased. Cooling the muscle on the other hand diminishes the strength of the current. Warm places in a fibre behave positively in reference to cooler ones.

The strength of the current which passes between two points of a muscular fibre is not influenced by the temperature of those portions of the fibre which lie between them. The changes in the electro-motive properties of muscle which are brought about by heat and cold disappear when the original temperature is restored (Hermann).

When the whole of a muscle whose external surface and artificial cross section are connected with the galvanometer is thrown into contraction, there is a cessation of the muscular current, a '*negative deflection*' (du Bois-Reymond). A single muscular contraction is not sufficient to overcome the inertia of the needle of the galvanometer, and to bring about the change in its motion which corresponds to the negative variation : the muscle must therefore be tetanised. Making use of the physiological rheoscope (p. 271), the negative variation can nevertheless be proved, in the case of a single muscular contraction, by causing the change in the intensity of the current to act as a stimulus to the nerves of a second muscle. (The nerve of the second muscle is brought in contact with the longitudinal and transverse sections of the first.) For every contraction of the first there is a contraction of the second muscle ('secondary contraction'). If the first muscle be tetanised, the second one also becomes tetanic (secondary tetanus), a fact which proves that in tetanus there are series of fluctuations in the intensity of the muscular current (p. 260). The '*negative deflection*' at the most amounts to a cessation of the current, there never being a reversal of its direction (Bernstein).

If the electrodes in contact with a muscle are so situated that, during rest, there is only a weak current, or an absence of current, it is observed that the corresponding variation in the intensity of the current, brought about by the contraction of the muscle, is in the first case very small, and that in the second there is no change (du Bois-Reymond).

When the nerves going to a muscle which is uninjured and, either approximately or entirely, free from electric currents, are excited, contraction leads to certain electro-motive manifestations, for which no general law has been yet found; the gastrocnemius, for instance, becomes the seat of a descending current which passes between the upper and lower tendons; similarly, during contraction, a descending current is observed in the unskinned lower extremity of the frog. During the voluntary tetanic contractions of the muscles of the human arm there is an ascending current, whilst a similar contraction of the leg is accompanied by a descending current (du Bois-Reymond). If muscular currents be present in the limbs whilst at rest, they add themselves algebraically to those just referred to as produced during contraction.

If a bundle of fibres is excited near one of its terminations, so that a wave of contraction runs along it (p. 261), it is noticed that the different spots in succession on the longitudinal surface become negative in reference to other spots, there being a negative wave, as it were, which travels along with the same rate as the wave of contraction, viz. about 3 metres per second (Bernstein). At each point the negative state, which first increases and then decreases, lasts about $\frac{1}{300}$th of a second; it is entirely gone by the end of the 'latent period,' which lasts $\frac{1}{100}$th of a second. Every point in a fibre must therefore first of all undergo electrical changes before contracting (Helmholtz, Holmgren); or, in other words, the wave of muscular contraction is immediately preceded by a negative wave. This wave of negative tension diminishes in intensity as it runs along (Bernstein).

For the methods by which these results were obtained, consult Chapter IX.

The magnitude of the fluctuations in the intensity of the muscular current depends precisely upon the same conditions as the magnitude of the excitation.

The two following opposed hypotheses serve to explain the electro-motive phenomena of muscle.

According to some (du Bois-Reymond), every muscular fibre contains in its interior electro-motive molecules, which are suspended in regular order in a conducting fluid. As these molecules altogether present positive surfaces towards the

longitudinal sections, and negative surfaces towards the transverse sections of a muscle, the former possess positive and the latter negative electrical tension. Every cross section, or the action of caustics, &c., lays bare new negative surfaces. During contraction or, rather, during the latent stage which precedes it, the electric-potential of these molecules diminishes, so that during the complete contraction of a muscle its current diminishes as a whole, whilst during partial contraction the tract of the muscle which is involved in contraction resembles in its behaviour an indifferent conductor, which now, in virtue of the negative elements of the portion of fibre at rest which are contiguous to it, comports itself negatively in reference to the remaining portion of the fibre. In order to explain how it is that the natural terminations of the muscular fibres do not behave (as they ought to do if the above-mentioned scheme held in its entirety) exactly like an artificial cross section, it is assumed that in contact with the ends there is a layer of abnormally arranged ('parelectronomic') elements, which present positive, and not negative, surfaces towards the natural cross section; the greater the number of these elements present the more free is the muscle from electrical currents, or the direction of the current may even be reversed. The development of parelectronomic elements, which, however, are never entirely wanting, is, as must be assumed, promoted by the action of cold, &c. In order to explain the deportment of uninjured muscles which are thrown into contraction, it is assumed that the parelectronomic elements of a muscle are not influenced by activity in the same manner as the other elements.

The other hypothesis (Hermann) refers all the phenomena to the effects of contact. There are two sets of circumstances under which muscular tissue comports itself as electrically negative with respect to living, inactive muscle, viz.: (1) when it is dying (entering into rigor), and (2) when it is in activity, or, more exactly, during the latent period preceding contraction.

The former case is taken to explain the negative state of every *artificial* cross section of a living, inactive, muscular fibre with respect to its exterior, for, at every artificial cross section between the already dead, and therefore indifferent, portions of the muscular fibre and those which are still living, there is

found a layer just in the act of passing into rigor. Hence, all the phenomena of the currents of muscle at rest (p. 272) are explicable. The latter case is cited to explain all the phenomena of muscle after stimulation, especially the diminution of the muscle-current on irritation of the injured fibre *in toto*, and the negative condition of the wave of contraction with respect to the rest of the muscle-tube. The fact that muscles destitute of currents, when acted on by stimuli proceeding from nerves, exhibit currents of definite direction between two electrodes, may be due to the circumstance that the waves of contraction running through the fibre from the point of entrance of the nerve reach the two points with different intensities, due, for example, to the different distances they are from the point of entrance of the nerve. In such a case the point where the wave was more intense would be negative to the other.

The two hypotheses above enunciated agree equally well with the facts. The second theory, in addition to its simplicity (it being necessary in the first (du Bois-Reymond's) to make at least four entirely independent assumptions), has in its favour that it brings into complete analogy the processes of rigor and activity, of which more will be said hereafter; and that the electrical currents exhibited by glands containing blood (p. 52) as well as by sections of plants, are capable of explanation in exactly the same way.

The above-mentioned influence of temperature, according to the first hypothesis, would have to be enunciated thus : That heat increases and cold diminishes the energy of the molecules. According to the second hypothesis it would, on the other hand, be necessary to assume that electricity was developed by the contact of warm and cold muscular substance, in which development the colder became negative.

Concerning the effects of electrical currents upon muscles reference should be made to the chapter on Nerves (Chapter IX.)

e. Interdependence of the Phenomena of Muscle, and Theories of Muscular Activity.

No satisfactory explanation of all the phenomena exhibited by muscle as yet exists. The most enigmatical of these phenomena, the diminution in length after stimulation, has hitherto been regarded by most thinkers as a sudden approximation of the smallest particles of the muscle in a longitudinal direction, the ultimate cause of which is a suddenly increased combustion. Many have, moreover, supposed quantitative relations to exist,

between the three forms in which kinetic energy may manifest itself in muscle, viz. mechanical work, heat, and electricity, of such a nature that (1) the sum total of these manifestations is greater during states of activity than during states of rest (during which, as a rule, none of the three forms appears to exist); that (2) any increase in one of the modes of manifestation is always correlated with a diminution in another.

None of these suppositions has, as yet, a basis in fact. It is especially doubtful whether, with equal stimulation, an increase in the amount of mechanical work done is accompanied by a diminution in the formation of heat. If the work done be varied by altering the weight to be lifted, the chemical processes which occur on contraction are also altered in extent, the amount of acid and substances soluble in alcohol, for example, increasing with the load (Heidenhain, Niegetiet and Heppner)—a circumstance which certainly does not agree with the supposition above named : the amount of heat generated *plus* the amount of work done (corresponding to the exchange of matter) vary with the load. Again, stimulus and load remaining the same, the work done may be varied in one of the following ways: Firstly, the weight may be allowed to fall freely to its former position after each lift has been accomplished, so that no available work is done, while the muscle is heated by the stretching due to the sudden fall of the weight. Secondly, the contracting muscle may be allowed to raise the weight higher and higher, by means of a wheel and axle arrangement, the weight being held by a catch during the intervals between contraction, real work being in this way effected (Fick). In the former case the muscle is certainly warmer than in the second ; but it may be objected (Heidenhain) that the chemical processes of contraction do not terminate with the lift, but rather continue during the succeeding extension of the muscle, and are then, as during contraction, influenced by the tension. It is a fact that the muscle generates less acid in the former case than in the latter (Landau and Pakully). Thus, again, the conditions of experiment determine the interchange of material, and therefore the sum of the work done *plus* the heat generated. It is, of course, undoubted, according to the principle of the conservation of energy, that the sum of the forces set free in muscle is, in every case, equivalent to that of the chemical decompositions which occur.

The analogy, which is now complete, between the phenomena of rigor and of activity warrants the proposition of a new theory of muscular contraction (Hermann) which differs from the views previously held. The points of analogy between rigor and the active state are the following : 1. The chemical process, so far as is known, is the same in both conditions (p. 252 *et sq.*). 2. In both acts the muscle shortens and thickens, its volume diminishing, and its electrical phenomena becoming less marked (pp. 244, 256). 3. In both acts

heat is generated (p. 268). 4. In both acts the contents of the muscle-tubes comport themselves electrically negatively towards unaltered (living and resting) muscle (p. 277). In muscle, which is entering into rigor, contraction of length is attributed to the coagulation of myosin, since it is well known that every albuminous tissue, *e.g.* a tendon, contracts strongly in the direction of its fibrillation on coagulation such as occurs on the application of heat. As now the supposition that contraction in a living muscle is accompanied by a sudden and transitory coagulation is not contrary to any of the known facts, we may assume such a coagulation to take place on the grounds of the analogy between rigor and contraction. Moreover, the following circumstances seem to favour such an assumption. There are no grounds for supposing that any conversion takes place in muscle of heat into motion (as in a steam-engine), or of electricity into motion (as in an electro-magnetic machine). There remains, therefore, only one possibility, viz. that of a direct origin of motion from the chemical decompositions which occur in muscular tissue. We can only imagine such a process to take the form of the production in consequence of chemical change of a new body, which endeavours, like the gases evolved on the ignition of gunpowder, to fill by elasticity a definite volume. That such is the case in muscle is already affirmed by Weber's theory (p. 262), and we may very well suppose the new body to be due to a sudden coagulation of albuminous substance, the explanation of details being as easy in this case as in that of contraction of tendon on boiling. The heat and electricity generated in muscle, from the quantities in which they occur, are at all events by-products. It is not yet decided whether they are dependent upon the processes of chemical decomposition, or upon physical changes of aggregation.

If contraction really depends upon a coagulation of the muscular contents, the coagulum formed must be capable of immediate disappearance, and in tetanus, of an alternate disappearance and reappearance several hundred times in a second. The above-mentioned process of synthetic restitution (p. 254 *et sq.*) is insufficient to account for this, as muscle, even during complete deprivation of oxygen, becomes again lax after each contraction. Moreover, that process does not affect firmly coagulated myosin at all. We may imagine that under stimulation the process of decomposition referred to on page 253 is suddenly very much accelerated, and that the myosin is generated with such rapidity that it has not time to pass at once into the state of

gelatinous solution, but enters for a moment into the undissolved condition which does not appear, under slower decomposition (*rigor*), until after considerable concentration. The fact that only very sudden stimuli are able to produce irritation in muscle seems to favour this view.

Although the view of muscular contraction just enunciated leaves much to be desired (the significance of the muscle-prisms or sarcous elements, for example, being provisionally quite unexplained), it seems to be a closer approximation to the true state of things than any of the older, purely physical, theories.

The production of heat does not probably depend entirely upon the processes of decomposition, but is, in part, a result of the synthetic processes of oxidation. These processes must be accompanied by manifestations of energy, and as they proceed during states of repose as well as during activity, being, however, increased in the latter condition, everything seems to imply that they are characterized by a development of heat. Muscle at rest may therefore be one of the chief seats of heat-formation. Finally the relative amount of heat produced in muscles cut out of the body renders it impossible that these processes of oxidation which then occur in traces should alone be the source of the greater part of the heat formed.

The uses of voluntary muscles in the body will be described in the Appendix to this chapter.

The sensory powers of muscle are discussed in Chapter X.

b. Smooth Muscles.

The 'smooth' or 'organic' muscles occasion the less energetic and slower movements of those organs, especially the alimentary viscera, which are not subjected to the influence of the will. They form, for the most part, membraniform expansions of varying thickness (*tunicæ musculosæ*), which are always fibrillated in a definite direction, and often so as to be divisible into layers. These expansions consist of long, spindle-shaped elements, which lie with their longitudinal axes in the direction of the fibrillation. The spindle-shaped elements do not, like the elements of transversely striated muscle, each run the whole length of the fibrillated tract, but they are arranged in rows, end to end. They are regarded as elongated cells which are not known certainly to possess a membrane (sarcolemma), but which contain a somewhat long nucleus. The latter is said by some observers (Frankenhäuser) to be at the same time a nervous end-organ, though others (Schwalbe, Arnold, Hertz) deny this. The cells never exhibit any trace of

transverse striation, but there is sometimes an indication of a striation in a longitudinal direction.   They are called 'smooth muscular fibres' or 'contractile fibre-cells.'

An examination in polarized light shows that smooth muscular fibres also contain doubly refractive bodies (disdiaclasts), which are not, however, arranged so regularly as in transversely striated muscle, but are scattered throughout the whole mass, so as to give the whole fibre the appearance of being doubly refractive (Brücke).   According to more recent theories (Engelmann) the division of the masses of smooth muscle into spindle-shaped elements is considered to be a phenomenon of death, and not to be pre-existent.

The chemical constituents of smooth muscular fibres are apparently the same as those of transversely striated muscle. The existence of a spontaneously coagulable substance may be assumed from the circumstance of the occurrence of death-rigor. As their reaction is constantly neutral or alkaline (du Bois-Reymond), it cannot be decided whether rigor in this case is accompanied by the formation of an acid ; since an acid might be generated in quantity insufficient to overcome the alkali present.   The muscles of the contracted uterus are acid to test paper (Siegmund).

The properties of the two classes of muscles are, as far as they have been investigated, almost identical; but the respiration, the chemical changes due to activity, the electrical conditions, the formation of heat, &c. of smooth muscles have not yet been made out.   The activity of smooth muscle manifests itself mechanically in the form of a diminution in length, which proceeds according to the same laws as in the case of transversely striated muscle (p. 256), but at a much slower rate—so much slower that the individual phases (latent period, gradual shortening and re-extending) may be perceived without any assistance; that is to say, after stimulation a considerable time elapses prior to contraction, which takes place very slowly, is maintained for some time at its maximum, and afterwards gradually disappears.   Where muscular bands exist (as in the ureter and intestine) contraction caused at one point may be seen to travel like a wave with a velocity of 20–30^{mm} per second, owing, apparently, to the direct conduction of irritation (Engelmann).   Automatic contractions have recently been stated to take place in the smooth muscles of the ureter (Engelmann).

Investigations of smooth muscles are very difficult, inasmuch as it is only possible to obtain sufficient material from warm-blooded animals, in which case it quickly loses its irritability.

II. CONTRACTILE CELLS. PROTOPLASMIC MOVEMENTS.

The contractile substance, protoplasm (p. 237), occurs inclosed in tubular sheaths (in muscle) and also in free, wall-less conglomerations, forming finely granular, and for the most part, microscopic masses of very variable form, and including nuclei. Such contractile masses form the whole substance of the body of many of the lower forms of animal life (Amœbea, &c.), or the soft portions of such animals (Rhizopoda); colourless blood-corpuscles, and the analogous corpuscles of connective-tissue, lymph, spleen, mucus, and pus in the higher animals (pp. 42, 81, 179); and the contents of many elementary parts of vegetables (cell-capsules).

All these protoplasmic masses are capable of general and partial contractions. The former follow on stimulation by means of induction-currents. The mass takes on the globular form where it is possible, and where it is not (*e.g.* when the mass is enclosed in a tube), approximates to that form as far as practicable by shortening and thickening (Kühne).

Partial contractions are, however, far commoner, and constitute, perhaps, the only kind which ever occurs in a normal condition. They may produce most manifold changes of form, such, for example, as the protrusion and retraction of processes [1] whereby foreign granules may be dragged into the midst of the mass; movements of the whole structure from place to place effected by means of the processes (*pseudopods*); movements of the granules, &c. in the interior of the mass; dancing movements (*molecular movements*); the excavation in the interior of the mass of spaces (*vacuoles*) which become filled with fluid. All these forms of movement have been frequently observed (M. Schultze, Brücke, Häkel, Kühne, von Recklinghausen).

[1] The protrusion of a process can only be explained by supposing contraction to be exerted along the direction of a chord, whereby a segment is pressed outwards. The process becomes long and thin in consequence of the repetition of the contraction along the various chords in the same segment one after another.

Molecular movement has been more exactly studied (Brücke) in the granules of the following cells: colourless blood-corpuscles, pus-corpuscles, mucous and salivary cells, cartilage cells, and pigment cells of the frog. This form of movement is very generally found. Inasmuch as molecular movement is prevented by many influences which prejudice the life of the cells in which it occurs, and as it always disappears at death, it is clear that this phenomenon is not the same as the molecular movement of inorganic precipitates. The ' cells ' above mentioned are not structures possessed of cell-wall and fluid contents, but consist of a tough mass in which, according to certain indications, we must suppose a complicated system of excavations or canals to exist. The matter of the corpuscles when at rest is chiefly aggregated about their nuclei and frequently forms radiating processes towards the periphery. Induction shocks cause the cessation of motion, and afterwards a sudden diminution in the size of the cell with expulsion of granules. Molecular movement is, therefore, a complicated phenomenon, closely connected with the remaining appearances of vitality.

The stimuli by means of which these structures may be induced to activity are the same as in the case of muscle, as are also the conditions of irritability and death (Kühne). At a temperature of 40° C. a species of rigor occurs ; a temperature of 36° C. acts as a stimulus producing tetanus (and the globular shape). Deficiency of oxygen destroys the irritability of protoplasmic masses. This circumstance, which is not in agreement with the slight influence which oxygen has on muscles removed from the body, is explained by the relatively greater surface exposed in the case of the small masses.

All protoplasmic structures appear, therefore, to contain the same essential substance as muscle. Its decomposition takes place during conditions of activity, and slowly during repose, until rigor intervenes. Its regeneration is accompanied by an absorption of oxygen at the surface. The weakest acids —even carbonic acid—have a most important prejudicial effect upon all protoplasmic movements.

Certain protoplasmic structures which do not migrate, *e.g.* a portion of the connective-tissue corpuscles of the cornea, are connected with nerve fibres, irritation of which leads to contraction (Kühne, Lipmann, though others doubt it). The great majority are, however, totally independent of the nervous system ; and the stimulus which causes the movements is still unknown. These movements may be considered as automatic.

III. CILIATED CELLS AND SPERMATOZOA.

The superficial cells of the cylindrical epithelium which covers certain surfaces of the body in single or stratified layers are provided at their free ends with fine, structureless hairs or ' cilia ' which are constantly in motion. Such surfaces of the body are : the respiratory tract, from the entrance of the nose to the alveoli of the lungs : the female generative organs from the opening of the Fallopian tubes to the os uteri externum : the cerebral ventricles with their communications. In the case of these cilia, no liberation of energy by means of the nervous system takes place so far as is known. Their movements consist for the most part in an alternate bending and straightening ; but pendulous, conical, and other forms of motion are said to occur.

Spermatozoa may be regarded as vibratory structures provided with one cilium. The head corresponds to the ciliated cell, and the tail is the cilium. The movement is a lashing to and fro.

If movable particles appear on such a vibratile surface, they are gradually pushed forward in a definite direction. This direction proceeds, in the case of the respiratory and genital apparatus, outwards. In order to explain it we must suppose that the movement of the cilia in one direction takes place more rapidly than in the other, so that one forward push follows another, otherwise the particles would have regained their old position after each forward and backward swing. The application of this vibratile motion in respiration has been noticed ; for its use in the movements of the ovum consult the fourth Section of the book. Small bodies provided with vibratile cilia, such as many infusorians and spermatozoa, are able to propel themselves actively by means of them through fluids in which they may be placed.

The circumstances which influence the movements of ciliated cells and spermatozoa are exactly the same as in the case of protoplasm (Roth, Kühne, Engelmann). The conditions necessary to its occurrence are : the maintenance of the state of concentration of the fluid bathing them ; the presence of oxygen (Kühne, according to Engelmann they can do without oxygen

for long periods of time) ; and a medium temperature. Increase of temperature accelerates their motion (Calliburces), as also do variations in electrical currents (Kistiakowsky). Very low or very high temperatures cause a stand-still (cold- and heat-tetanus) which gives place to movement on a return to the normal temperature (Roth). At a temperature of 45° C. a permanent stand-still, *rigor*, is produced, with acidification. Rigor occurs spontaneously after removal from the body. The action of acids is very prejudicial to ciliary movement as well as to the movements of protoplasm. The effect of alkalies in restoring the power of vibration to cilia in which it has spontaneously disappeared (Virchow) merely consists, therefore, in all probability in the neutralisation of prejudicial acids (Roth). Other observers, however, ascribe similar reviving powers to acids, alcohol, ether, &c. (Engelmann).

The vibratile movements of ciliated cells and spermatozoa are therefore, most probably, but a special modification of the movements of protoplasmic masses. It is not yet decidedly known whether the cilia are passive and merely moved by the protoplasm of the cell, or whether they also, being themselves of a protoplasmic nature, actively assist.

APPENDIX TO CHAPTER VIII.

THE USES OF MUSCLES.

The property of muscles to shorten or contract is made use of in the most varied manner in order to bring movable parts towards each other, out of their position of equilibrium, so as to produce changes in the form of the body. The position of equilibrium of the parts of the body is dependent on various mechanical causes, chiefly gravity and tension (elasticity). Changes of form either take place for purposes subject to the will (voluntary movements), or they are brought about by certain mechanisms, which have their seat in the central organs of the nervous

system (involuntary movements). The form-change caused by the shortening of a muscle (or of a single muscular fibre, which may be taken as a type of the entire muscle) may be determined in every case, if the position of equilibrium and the degree of mobility of the parts to be moved, and the position of the muscle itself, are known. We have here to consider chiefly two forms of muscular effort. 1. The two terminal points of a muscle are connected together and therefore not movable towards each other. Here a shortening of the muscle can only take place when the muscle does not stretch in a straight line, but between its two points forms a curve. This is the case with the hollow muscular organs, where the muscular fibres run along on a cylindrical, spherical, or otherwise curved surface, either with their ends joined (directly, or by the juxtaposition of many fibres), or with their ends acting on a body which may be considered fixed (intestine, heart, uterus, bladder, &c.). In this case a tendency to approach a straight line is manifested during the muscular contraction, and hence the surface on contracting exerts a pressure on the fluids which may be contained in these hollow organs. 2. The end-points are movable in reference to one another, being either both movable or (as is commonly the case) one movable and one fixed. In this case the contraction of the muscle, supposing it to be stretched between its two terminal points, causes these end-points and all the parts to which they are fixed to approach each other. In the case in which one of the two points is fixed the other alone will move; if, however, both are movable, then the changes are inversely proportional to the resistances acting in opposition to the movement. The direction of the movement does by no means always lie in the straight line joining the two points. Deviations from this direction are caused: *a*, when the course of the (stretched) muscle or its prolongations (tendons) is not straight, but either curved or bent (when, for instance, the muscle or tendon runs over a pulley-like projection); *b*, when the two fixed points cannot move towards each other in a straight line, their extent of motion being limited by some mechanism or other. In the latter case the whole of the kinetic energy of muscular action (which is determined by the length, section, and degree of activity of the muscle) is not employed in bringing about changes of position, but a part of it is, by the resistance of the me-

chanism, converted into heat. The part used in changing the form is easily determined by the parallelogram of forces, according to which it is split up into two component parts, the one in the direction of the absolute resistance, the other in the direction of the absolute mobility; the latter of the two components represents the amount of form-change.

Let ac and bc be two bones which are connected by a hinge-joint c, and movable towards each other by the muscle de; ac being considered fixed,

Fig. 8.

then the point d can only be moved in the direction dg, vertical to bc (the tangent of the arc di). The force of muscular contraction is therefore to be resolved into the two components dg (the moving portion, or the form-changing portion) and dh (the direction of the absolute resistance, or the portion which represents the pressure on the joint). It will be seen at once that as the contraction increases the moving portion, d_1g_1, increases, while the other portion, d_1h_1, diminishes. If now we call к the force of traction of the muscle, then that portion of к which is effective $=$ к sin cde, and the moment in relation to the lever-arm $cd =$ к. cd, sin cde; but $cd = \dfrac{ck}{\sin cde}$; the moment therefore $=$ к.ck; *i.e.* the muscle acts at every instant as if it acted with its full power on the arm of a lever, the length of which is equal to the shortest distance of the joint from the muscle (Henke).
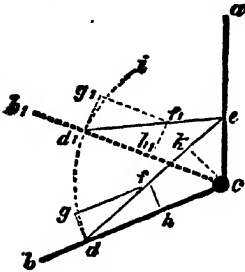
The conversion into heat of that portion of the work done by the muscle which exerts pressure on the joint is to be taken in the sense, that the pressure on the joint increases the friction, whereby the evolution of heat normally due to this cause is increased.

Those muscles which act on rigid parts of the body (bones, cartilage) act almost always as on levers, since the rigid parts are nearly all arranged so as to be movable around a point; hence also the constitution of the momentum of the muscular action as regards weight and velocity will become variously modified. Most of these levers belonging to the second and third kinds, *i.e.* the point of traction of the muscle (power) and the resistance (weight) are on one and the same side of the fulcrum; levers of the first kind are, however, also found, as, for instance, in the forearm, where the triceps acts on the olecranon. The point of traction of the muscle (the power) is generally situated near the fulcrum, and the power-arm is thus much smaller than the weight-arm, and hence only small weights (considered to act at their natural point of application)

can be moved, but with great velocity. This arrangement enables us to perform the different movements of the body with great rapidity, and obviates also the clumsy form which our body, particularly the extremities, would have to take under the opposite arrangement, as will be easily understood on reflection.

Where more than one muscle act in different directions on the same part, or where only one muscle acts, the fibres of which, however, have different directions, the resultant can always be easily found by the parallelogram of forces. When different muscles acting on the same part are so arranged that the resulting motion due to the simultaneous action of all becomes = 0, that is, the part acted upon remains at rest, then each of these muscles is called the *antagonising muscle* of the rest. The position of equilibrium of any part of the body acted upon by antagonising muscles is, apart from the effect of gravity, that position in which the elastic forces of all muscles balance each other.

We have already spoken of some of the special uses to which muscles are applied in the first Section, particularly when considering circulation, digestion, and respiration. In this chapter we shall consider in a general way the movements of the rigid parts of the body, bones and cartilage, which are so connected with each other as to admit of motion, and then study separately two important groups of motion, namely, 1, the locomotion of the entire body, and, 2, those movements in the passage of entrance to the respiratory apparatus, which serve for the formation of voice and speech.

Mechanism of the Skeleton.

The elements of the skeleton—the bones—are for the most part movably joined to each other. An exception to this is seen in the connection of the bones by *sutures*, such as are found in the cranial bones, which render the bones absolutely immovable for all such forces as do not endanger the existence of the organism ; such bones are then to be considered as forming an immovable mass. Amongst the movable connections of bones we distinguish two kinds : the first of these—the *synchondroses* and *symphyses*—allows but a very slight movement, yet fairly

unlimited as regards direction; the combination resulting
from this junction is of stable form, to disturb which requires
a very strong force and into which the bones, as soon as that
force ceases to act, spring back by virtue of their elasticity.
The second kind—the *movable joints*—allows of a free move-
ment without any material resistance, a movement which is,
however, limited as regards direction ; this form, therefore, has
no definite position of equilibrium.

Synchondroses.

The *synchondrosis* is formed by the connection of two
opposed, generally congruent, bony surfaces by means of an
intermediate more or less solid connecting substance, mostly
hyaline or fibro-cartilaginous. Ligamentous sheaths at the
place of junction prevent the lateral displacement of this
connecting substance. The degree of mobility of this joint
depends (1) on the absolute strength of the connection; (2) on
its dimensions, for the mobility is (independently of the liga-
mentous sheath) directly proportional to the *thickness* of the
connection, *i.e.* the distance of the two bone surfaces from each
other, and inversely proportional to the *transverse diameter* of
the connection, *i.e.* the size of the two opposing bone surfaces;
(3) on the rigidity of the surrounding ligamentous band. The
mobility of these joints is in all cases very small and muscular
traction has therefore scarcely any effect on them ; their elas-
ticity is, however, of great importance ; especially is this the
case with the spinal column, in which we have a series of syn-
chondroses (the intervertebral cartilages) in virtue of which
this curved column is endowed with a certain amount of flexi-
bility and great elasticity.

Movable Joints.

In these joints the causes opposed to motion are reduced to
a minimum; the direction of the movements is, however, by
the form of the joint, limited in various ways. The two bones
entering into a joint oppose to each other smooth surfaces,
covered with cartilage (the articular surfaces), which are con-
stantly kept in apposition with each other, over as wide an
area as possible, by certain means which will be described pre-

sently. The one of the two articular surfaces is always larger than the other.

The most simple joints are those in which the smaller articular surface is always everywhere in contact with the larger. Where this contact is permanent, there can be no other but a gliding movement of the smaller articular surface on the larger; the relative movement of the two bones then depends entirely on the form of the articular surface (as one surface covers the other, the one is the exact cast of the other). In general only certain surfaces of regular form will allow such a gliding movement, and these surfaces are : 1. Plane surfaces (joints of this kind seem not to occur, but the movements which they would allow are: *a.* Rotation of each of the two bones round axes which are perpendicular to the plane of the joint. *b.* Movement of the axis of each bone parallel to itself). 2. Parts of surfaces of rotation, *i.e.* surfaces which may be conceived to have been formed by the rotation of a straight line or of a line of single curvature round an axis lying in the same plane. In this manner, if the rotating line be a straight line parallel to the axis the articular surface is a cylinder; if it is a straight line, but not parallel to the axis, a cone; if it is a semicircle and the axis its diameter, a sphere; if it is a segment of a circle and the axis on its convex side, it is a surface of saddle-form; if the axis is on the concave side forming a chord, a cycloid; if it is an ellipse and the axis one of its geometrical axes, an ellipsoid, &c.; lastly, if it is any other curved line, the articular surface is that of some pillar-like, turned, body, &c. All joints of this description allow of a rotation of both bones round a common axis, the geometrical axis of the articular surface; they are called *uniaxial* or *hinge-joints* (Ginglymi). An exception to this, however, is presented by those joints whose articular surfaces are parts of a sphere; they allow a rotation around any diameter of the sphere, or, as it is said, round a point, namely, the centre of the sphere; these joints are called *multiaxial* or *ball-and-socket joints* (Enarthrodia). In the *screw-joints* we have a uniaxial joint of peculiar construction. Here the articular surface may be thought to have been formed by the rotating line (which is here a curved line) advancing in the direction of the axis, during the rotation, with a velocity which is propor-

tional to the velocity of rotation. Joints of this description cause an opposite movement of the two articular surfaces around the axis (analogous to the movement of the screw turning within the nut).

The conditions which have just been the subject of consideration are only found in some of the joints of the body, and not even there with mathematical precision. In a great many of the joints the surfaces are not congruent, and a perfect contact of all the points of the smaller of the two articulating surfaces is therefore impossible. Again in some of the forms spoken of we notice positions in which the apposition of the surfaces is imperfect; such a condition of things, for instance, enables joints with saddle-shaped or cycloid surfaces to admit of rotation round two axes; to wit, round the axis of rotation, and round a second axis which passes through the geometrical centre of the rotating arc and is vertical to the axis of rotation, provided always that the one surface covers only a small part of the other. Wherever the two articulating surfaces are not in contact the spaces are filled up by soft parts or fluids (see below.)

Wherever a perfect congruence of the articulating surfaces is not required, the variety of joints and the movements of which they are capable increase beyond measure. It is therefore impossible to draw any conclusions from the mere shape of the two articular surfaces, as to the degree of movement allowed; for the limitation of movements will chiefly depend on the other factors. A general consideration of these irregular joints, whose surfaces are not those of rotation, is therefore impossible; but to consider each one separately would lead us too far.

Mechanism for Maintaining Contact.

The constant and close contact of the two articular surfaces is effected by the following means. 1. The space between the two surfaces is closed, for the ends of both bones are connected by a short tube (the synovial capsule), which is attached round the articular head of each of the two bones; the cavity which is thus formed has only a capillary lumen and is filled with a tenacious lubricating fluid (*Synovia*). The two articulating surfaces can separate no further from each other than the small quantity of

synovial fluid will allow, and every further separation is pre-
vented by atmospheric pressure, which presses with a force
equal to the product of the surface-capacity of the smaller
articular surface and the barometric pressure for the surface-
unit. This mode of contact is of importance in joints with
large surfaces, especially in the ball and socket joints, where
any other mode of attachment would restrict the free mobility
in all directions. In the hip-joint, the largest ball-and-socket
joint of the body, the smaller articular surface (that of the
acetabulum) is of such a size, that the atmospheric pressure
balances the weight of the whole lower extremity, so that even
after all the soft parts surrounding the joint are separated and
the synovial capsule cut through, the lower extremity does not
drop out of the socket (the brothers Weber); the surface of
the acetabulum is further increased and the closure of the joint
ensured by a thin-edged elastic cartilaginous ring (Labrum car-
tilaginium) which surrounds everywhere the free margin of the
acetabulum and attaches itself closely to the head of the femur
in all movements. Where the articular surfaces cover each
other but very imperfectly and the joint-cavity is thus con-
siderably increased, we have the greater part of this cavity filled,
not by synovia, but by movable cartilage, masses of fat and
ligaments which pass through the joint; the best example of
this form is the knee-joint. 2. In nearly all joints ligamentous
masses serve to fix the joint; these masses consist either of
stretched bands, which run from one bone to the other (in most
cases attached to the capsule) or in stretched parts of the cap-
sule itself. As these fixing bands have always to be in a state
of tension, they must be so placed as not to hinder movement;
with hinge-joints they are therefore always found at both ends
of the axis of rotation. In most joints where the surfaces are
incongruent (*i.e.* do not cover each other) the axis of rotation
is only determined by the insertion of the fixing ligaments.
3. The tension of the surrounding muscles plays an important
part in holding the articular ends in apposition.

Check Mechanisms.

The appliances which determine, not the direction, but the
extent of articular movements, are these: 1. A particular con-

figuration of the *bone*; thus, for instance, the abutting of the olecranon against the sinus maximus of the humerus restricts the extension of the forearm. 2. So-called check-ligaments, *i.e.* ligaments which become stretched in extreme positions of the joints by being so attached that the distance between their two extremes increases to a maximum with the movement of the joint (in joints also where bones restrict the extreme movements we have often ligaments which limit the movement still more). One form in which ligaments which maintain contact act as check ligaments occurs in so-called *spiral joints*, of which the knee-joint forms a good instance. A horizontal section through the articular end of the femur shows as external limit a spiral, the centre of which is situated posteriorly, while its vectors increase in length as they proceed from behind forward. The upper ends of both lateral ligaments are attached to the terminal points of an axis passing transversely across the centre of the spiral (tuberositas condyli interni and externi femoris); the lower end of the internal ligament is attached to the condylus internus tibiæ, that of the external to the head of the fibula. These two ligaments make the knee-joint an imperfect hinge-joint, but inasmuch as with flexion of the knee the smallest vectors of the spiral, and with progressive extension, progressively larger vectors, are moved in the direction of the ligaments, so the distance of their points of insertion, and therefore also their tension, increases as the knee passes from flexion into extension, the tension reaching a maximum, beyond which further extension is impossible. This arrangement it is which renders possible the rotation of the fore-leg round its vertical axis independently of the thigh only during flexion of the knee, and not when the lower extremity is extended, in which case the thigh and fore-leg being wedged in at the joint form but one piece. 3. The soft parts also (muscles, tendons, and skin) surrounding the joints assist by their tension to limit the movements in a manner similar to that of the check-ligaments.

It happens occasionally that when a muscle runs over two joints, the flexion or extension of one of these joints stretches the muscle in such a way as to make it a sort of check ligament for the other joint : this is called 'passive insufficiency,' in contradistinction to 'active insufficiency,' by which is meant the opposite condition, in which flexion or extension of the one

joint slackens the muscle in such way as to make its contraction have no effect (C. Hüter, Henke).

Conditions of Equilibrium and of active Locomotion of the whole Body.

It will be found convenient for the relations which are to be considered under this head to look upon the body as a chain, with many links and various branches, the joints of which are to be looked for where two bones are movably connected. Such a chain can only be in a stable equilibrium when each joint is sufficiently supported. This will be effected in different ways in the different positions of the body (lying, sitting, etc.). The positions which will be considered here are the erect posture and the sitting posture.

The Erect Posture.

By the free erect posture we mean that position of equilibrium in which the whole body rests entirely supported by the two feet touching the ground. If now the body were a rigid, unjointed pillar, the only condition to be fulfilled would be that the centre of gravity should be supported by the basis or surface of support (which is given by the points of contact between the soles of the feet and the floor), or, in other words, that the line of direction of the centre of gravity should meet the floor within the basis of support. The human body can only be made into such a rigid pillar by having all the movable articulations immovably fixed. In the natural erect posture this is effected almost without any muscular effort, the muscles coming in use only to supplement the somewhat unstable equilibrium.

The articulations to be considered here are the tarsal and tarso-metatarsal joints, the ankle-joint, the knee-joint, the hip-joint, the articulations of the vertebræ (the symphyses of the pelvic bones may be considered as absolutely fixed) and the articulation between the head and the uppermost cervical vertebræ. The other articulations (those of thorax, upper extremity and jaw) do not enter into consideration here, for the bones to which they belong are merely appended to, without in any way serving for the support of, the other bones.

1. *The joint between the head and the uppermost cervical vertebræ.*—The two surfaces of the atlas which articulate with the occipital bone form parts of one curved surface with concavity upwards, the curvature of which is slighter anteroposteriorly than laterally. The joint is, therefore, biaxial, *i.e.* the sagittal axis of rotation is situated higher in the head than the frontal, and the greatest amount of motion takes place about the latter. The joint allows also a rotation of the head on the atlas during forward flexion. The most important rotation of the head, however, occurs at the odontoid articulation between atlas and axis. In this joint the odontoid process of the latter vertebra forms a vertical axis of rotation for the atlas and skull. The articular surfaces of the superior oblique processes of the axis are seen, in a sagittal section through atlas and axis, to be convex towards their articular cavities. Therefore, in the mean symmetrical position, the head must be highest, and must glide somewhat downwards, on lateral rotation, like a screw. This arrangement probably guards against torsion of the cord when the head is rotated from side to side. While, in the joints about to be considered, every care seems to be taken to expend as little muscular energy as possible, and to gain the required objects by mechanical means, the great freedom of the axial, atlantic, and occipital articulations requires that the position of the head should be determined by the muscular effort of the numerous muscles attached to it. If this effort is wanting (as, for instance, during sleep), then the head in the erect posture inclines forward and rests with the chin on the chest, for its centre of gravity is in front of its point of support.

2. *The vertebral column.*—The vertebral articulations are chiefly synchondroses; the vertebral column forms therefore a rigid, somewhat flexible and exceedingly elastic rod, variously curved (with the convexity in front in the cervical and lumbar regions, and with the concavity in front in the dorsal and sacral regions). The mobility of the vertebral column, which is quite wanting in the sacral region, increases from below upwards, owing less to the diminished transverse section of the intervertebral cartilages—for this circumstance, otherwise of advantage for movement, is neutralised in its effects by the simultaneous diminution in the thickness of the cartilages—than to

the constitution of the true joints between the oblique (articular) processes. In the lumbar region these articular surfaces are nearly vertical, sagittal, and almost parallel (being slightly convergent forwards), so that each upper vertebra is locked in the one below ; rotation about a longitudinal axis is, therefore, quite prevented, while flexion, antero-posterior, or lateral, is possible only in the slightest degree. In the dorsal region the surfaces of articulation of the articular processes are more antero-posterior in aspect, converging posteriorly, and permitting, therefore, a. lateral rotation ; lateral flexion, also, is not entirely prevented, but antero-posterior movement is quite impossible without a disengagement of articulating surfaces. In the cervical region the articular surfaces become more and more horizontal, and allow of movement in all three directions.

3. *The hip-joint.*—*a.* The centre of gravity of that portion of the body which is to be supported by this joint (head and trunk) is situated near the vertebral column (in front of the tenth dorsal vertebra), in a horizontal plane passing through the xyphoid process (Weber) ; it will of course vary somewhat with the degree of distension of the digestive canal. A plumb-line let fall from this point (the line of gravity) passes behind the line of junction of the hip-joints, and the trunk would therefore in the erect position fall backwards, but for its attachment anteriorly by the ilio-femoral ligament to the femur (linea intertrochanterica anterior). This balancing of the trunk on the heads of the thigh bones might thus be compared to the position of a gun obliquely supported over the shoulder, where the grasp of the butt end by the hand prevents its falling over. The action of the anterior part of the tense fascia lata (Lig. ilio-tibiale) and of the stretched m. extensor quadriceps is similar to that of the ilio-femoral ligaments, only with this difference, that they are attached to the leg. *b.* The trunk has also to be fixed in a vertical plane to prevent it falling either to the right or left; for as the two feet are not fixed to the floor, a falling over to one side, *i.e.* the rotation of the trunk around the head of the femur laterally, would be possible; this is, however, prevented by the ligamentum teres, which checks the adduction of the extended thigh beyond the middle line, and without such adduction, the lateral rotation of

the trunk spoken of cannot take place; this is particularly the case in the erect posture, where the ligamentum teres is already stretched by the eversion of the thigh and leg (this rotation outwards is due to the action of the gluteus maximus);—the external tense sheath of the fascia lata is another accessory to check adduction. *c.* It is unnecessary, as long as the body rests on the two feet, to provide against the rotation of the trunk on the head of the femur; this can, however, be effectually done by the glutei and the ligaments.

4. *The knee-joint.*—*a.* The common centre of gravity of head and trunk and thighs is situated somewhat lower than, but not much anteriorly to, the centre of gravity of head and trunk. The line of gravity will therefore here also pass *behind* the point of support of the knee-joint, but the difference is so slight that no great force is required to prevent falling over (flexion of the knee). The agents are the lig. ilio-tibiale (see above), the slight tension and contraction of the extensor quadriceps and the lig. ilio-femorale, for in order to flex the knee while the fore-leg is fixed the femur has to rotate outwards, which is prevented by the lig. ilio-femorale. *b.* There is no need of fixing the knee-joint laterally, as this is sufficiently insured by the hingelike nature of the joint (lig. lateralia). *c.* Rotation on the fore-leg during extension is prevented by the crucial ligaments, as described before, p. 294.

5. *The ankle-joint.*—The centre of gravity of the whole body (neglecting the feet) lies approximately in the promontory of the sacrum; the line of gravity will therefore pass a little in front of the line connecting the axes of both ankle-joints, and hence the falling forward of the body has to be provided against. This can be done, *a*, by the axes of the two ankle-joints forming an angle with each other, so that the simultaneous rotation round both is impossible without a change of position (separation) of the lower extremities; *b*, by the posterior and smaller part of the pulley-like articulating surface of the astragalus becoming wedged into the fork-like surface formed by the two malleoli, which, when the leg is extended, is so narrow as not to be able to receive the anterior and wider part of the trochlear surface of the astragalus (which would be necessary for the falling forward); this wedging in between the malleoli is brought about by a rotation of the tibia round the fibula, which

accompanies the final act of every extension of the leg,[1] whereby the fork-like cavity on the articular surface of tibia and fibula is so turned as to grasp the trochlear surface of the astragalus obliquely. *c.* By the contraction and tension of the flexors of the foot (in the anatomical sense), the muscles attached to the tendo Achillis, tibialis post.; peronei post., etc.

6. *The small joints of the foot.*—The tarsal and metatarsal bones form an arch, on the highest point (caput astragali) of which the weight of the body acts, and which rests with three points on the floor, viz. with the tuber calcanei (heel) and with the capitula of the first and fifth metatarsal bones (the ball of the big and of the little toe). This arch, which the weight of the body tends to flatten, is chiefly maintained by the tension of the ligaments on the plantar side of the foot; only when these ligaments are rendered pathologically lax, does the arch yield (flat foot).

The toes do not serve any purposes for support in the erect posture, but are of use in maintaining the balance, particularly in walking. 'Standing on tip-toe' is likewise only the balancing of the body on the capitula of the metatarsal bones, while the ankle-joint is extended (in the vulgar sense) and the trunk so much arched forward, that its line of gravity falls within the line of support.

The Sitting Posture.

In sitting, the trunk rests on the two tubera ischii like on the rockers of a rocking-horse (H. Meyer), and it can therefore swing forward and backward; we thus distinguish between an anterior and posterior sitting posture, according as the line of gravity falls either in front of or behind the line connecting the two resting points of the tubera ischii. In the anterior sitting posture the trunk is prevented from falling forward, *a*, by supporting it (resting the elbows on the table, etc.); *b*, by fixing it against the lower extremities, by putting the feet on the ground or supporting the thigh on the anterior border of the chair; the fixing is chiefly carried out by the extensors of the thigh. In the posterior sitting posture the trunk must rest

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[1] This rotation is due to the form of the knee-joint, for with every extension the two condyles of the femur roll forward on the articular surface of the tibia in the manner of a wheel, though not to the same extent.

against a posterior support, either with the back (high-backed chair) or with the lumbo-sacral region (low-backed chair), but the equilibrium can also be sustained without a support, in which case the point of the sacrum forms the third point of support. Lastly, by stretching the legs forward and fixing the trunk against them by muscular exertion, a position may be found, in which the centre of gravity of the whole is moved forward to such an extent that the feet form the third point of support; when, in this position, the trunk is moved slightly backward, the feet will leave the floor.

Walking.   Running.

In walking, the pelvis (and with it the trunk) is rhythmically and alternately supported by one of the two legs (the active leg) and dragged forward a certain distance (the length of a step), while the other (the passive) leg merely hangs on the pelvis. At the commencement of a step the leg which is to be the active leg during this step is placed vertically (slightly flexed, see below), and forms one of the two sides of a rectangular triangle, the hypothenuse of which is formed by the passive leg, stretched out behind and touching the floor only with the toes, while the line joining the feet on the floor forms the third side. The active leg now passes forward carrying the pelvis with it from its vertical position into an oblique (hypothenuse) position, but as the pelvis is to be moved horizontally forward, the active leg must necessarily be lengthened, and this is brought about by the extension of the leg (which we saw at the beginning was slightly flexed) in all its joints: the extension of the foot causes the heel to be lifted from the floor, whereby the point of support also moves to the capitula of the metatarsal bones, but these also are in their turn lifted from the floor, so that the leg only touches the floor with the extremity of the big toe; the foot is thus as it were raised from the floor like a chain, its separate joints being successively lifted from the floor. The active leg now occupies the same position in relation to the trunk as the passive leg did at the commencement of the step. Now the passive leg, which of course was the active leg of the step immediately preceding, leaves the floor at the commencement of the step and describes a

pendulum oscillation forward around its pelvic point of suspension, which brings the foot of the passive leg just as far *in advance* of the active leg as it was *behind* it at the commencement of the step (namely, the length of a step); the foot is now put down and comes to be just vertically under the pelvis, which in the meantime has been carried horizontally forward by the active leg, as we saw. (In order not to touch the floor while swinging forward, the passive leg is somewhat shortened by being flexed.) During the step the active leg has thus passed from its original position (that of one of the two sides) to the position of the hypothenuse of the rectangular triangle, the passive has moved from the hypothenuse position into that of one of the two sides of the triangle; the triangle is moved forward the length of one step; the passive leg has swung forward the length of the step, while the active leg has kept its position; both legs now change their ' part,' that leg which had been the active becomes the passive leg and commences its oscillations, while the passive leg, after being put down on the floor, commences its series of extensions, etc.

The rapidity of walking will therefore depend: 1, on the length of the step; 2, on the duration of the step, which is composed of the duration of the pendulum oscillation and the interval between its termination and the commencement of the next, or, in other words, the length of time during which both feet rest on the floor. 1. The length of step, considered as one of the two sides of the rectangular triangle, is the greater, the greater the difference between the hypothenuse and the other of the two sides of the triangle; therefore, *a*, the smaller, *i.e.* the more flexed the active leg is at the commencement of the step, or the lower the pelvis is carried ; *b*, the greater is the difference in length between the leg totally stretched (or totally lifted from the floor) (passive leg) and the leg planted vertically, or, in other words, the longer are the leg and foot—long persons therefore take longer steps than short persons:—2. *a.* The pendulum oscillation is, according to known laws, the quicker the shorter the swinging leg is ; the elongation (length of step) is likewise to be taken into account, for the angle of elongation here is relatively large. *b.* The interval of time during which both feet rest on the floor, can be shortened at will, and in very quick walking is $=0$; the extended foot therefore leaves the floor

exactly at the moment in which the other after being swung forward touches it.

A still greater velocity is obtained in the act of *running*, where there is an interval in the period of the step during which both feet are off the ground—the one (the extended) leg has already begun to swing forward before the other has finished its oscillation. The only thing essential here is that the pelvis should swing forward with sufficient velocity, so as to be prevented from falling during the time it is suspended in the air; this is effected by having the active leg at the commencement of the step strongly flexed, and stretching it with great, as it were, jerking velocity.

We cannot consider here the different varieties of walking and running and the necessary phenomena thereby observed (W. and E. Weber, H. Meyer), part of which are deducible from what is stated above.

Voice and Speech.

The stream of air which passes through the larynx and the cavities of the pharynx, mouth, and nose during expiration (and in exceptional cases during inspiration also), is made use of in order to throw into vibration portions of those organs and so to produce sounds and noises. To the sounds thus produced the term 'voice' is applied; and both sounds and noises when used as signs for intercommunication are called 'speech.'

1. Voice.

The sounds of the voice are produced by the vibration of the lower vocal cords of the larynx, which are stretched out after the fashion of a membranous tongue in the laryngeal tube. The stream of expired air is projected upon them from below; and the tube into which the vocal cords are fixed—formed below ('windpipe') by the bronchial tubes, trachea, and larynx, and above ('sounding pipe') by the larynx, pharynx, buccal and nasal cavities—serves, as is the case in reed instruments, partly to modify the sounds and partly to intensify them.

A *compound tone (Klang)* has recently been defined by Helmholtz as any auditory sensation produced by periodically regular vibrations. If the vibrations of the air are simple, like those of a pendulum, a '*tone*' is the result. The vibrations producing any complicated regular sound may be resolved by a well-known mathematical law into a number of simple, pendular vibrations, having the ratios one to another of 1 : 2 : 3, &c. (Fourier).

This resolution of a sound into its elements may be brought about not only mathematically, but also to a certain extent mechanically, in a manner which will presently be described. Every compound tone may therefore be considered to be an aggregate of simple tones, the numbers of whose vibrations are in the ratio of $1 : 2 : 3$, &c. The deepest of these tones is called the 'prime tone,' and the rest 'harmonics.' If the number of vibrations of the prime tone is n, those corresponding with the harmonics are $2n$ (the octave of the prime tone), $3n$ (the twelfth of the prime tone), $4n$ (the second octave), $5n$ (the compound), &c. The number of the partial tones of a tone, and their relative intensity, vary much in different musical sounds, as, *e.g.*, in the sounds produced by different instruments. It often happens that certain of the harmonics are wanting altogether. A musical sound is named after its most prominent partial tone. If any given tone, say A, occurs as the principal tone in different sounds, the latter are described as A accompanied by differences in 'timbre' or 'quality' (*Klangfarbe*). If the vibration of a compound tone be represented by a curve, the latter will be found to differ considerably in form from that of a simple tone; though it frequently approximates in shape to the wave of its prime tone. Hence it used to be said that two 'tones of different timbre,' of equal pitch and intensity, differed from one another in the characters of their representative curves or waves, which were, of course, of the same height and length in each case.

The resolution of a compound tone into its partial tones is most easily effected by means of resonators (Helmholtz). A simple *tone* is able to throw into sympathetic vibration almost all bodies which have the power of vibrating an equal number of times per second. Hence, any compound tone is capable of calling into vibration neighbouring bodies whose vibratory powers correspond with those of its partial *tones*; and, moreover, of causing them to vibrate with the relative intensity corresponding to the individual tones into which (according to Fourier's law) the sound may be decomposed. If, therefore, a sound with A as the prime tone were produced in the neighbourhood of a series of such resonators or bodies the vibratory powers of which correspond with the harmonics of the tone A, some of the resonators of the series would resound with varying intensities, while others would not sound at all. The simplest resonators are glass or metal globes of a certain pitch, provided with two openings, one of which communicates with one ear of the investigator, while the other ear is stopped. Whenever the tone to which the resonance-globe answers occurs in a sound, it is heard quite loudly by the person whose ear communicates with the globe, while he cannot hear the other partial tones. Just as a compound tone can be analysed into its partial tones, it is possible in a similar manner to build up a sound from its component parts. The methods of producing and combining simple tones will be explained in the section on speech.

In like manner the sounds produced by the larynx and analogous reed-pipes consist of prime tones and harmonics. The former are very marked, but as many as six or eight harmonics may be detected by the above method of analysis. In the following section, whenever the tones of the larynx and their pitch are spoken of, it must be understood that the *prime tones* are referred to.

Sounds of Reeds and Reed-pipes.

The word 'tongue' or 'reed' is used in acoustics to denote an elastic plate which, when at rest, nearly closes an opening, but which is so arranged that every excursion from the position of rest tends to increase the space between its edge and that of the opening. If a sufficiently powerful blast of air be blown upon the opening, the 'tongue' or 'reed,' as is easily seen, is thrown into vibration. That is to say, the space between the border of the opening and the edge of the plate, while the latter is at rest, is so narrow, that the stream of air is not able to pass through it in that condition, but experiences an obstruction. In consequence of this, the air accumulates behind the tongue, and presses upon it with a force which gradually increases, until a point is reached at which the elastic plate is forced out of position. This gives a passage to the accumulated air, which rushes through violently, and so reduces the pressure behind the tongue that the latter falls back into its former position ; whereupon the whole action is repeated. By this means a continuous stream of air is converted into an intermittent or rather a varying current, and the tongue thrown into vibrations. The sound resulting is really produced by the vibrations of the air (as in the instrument called the Siren) and not by those of the tongue (Helmholtz). The tongue may consist either of a firm elastic plate fixed at one side, as is the case in many musical reed instruments, or of an elastic membrane (membranous tongue) stretched over the opening. If of the latter kind, the membrane may be so fixed as to leave spaces at both sides, or it may completely cover the opening, with the exception of a slit in the centre. The larynx, with its vocal cords and glottis, answers to the last-mentioned description.

The pitch of the note given out by a tongue vibrating under the influence of a current of air (*i.e.* the number of vibrations per second necessary to produce it) depends upon the time of vibration of the plate itself, as by that is determined the frequency of the impact of the air. The time of vibration of the plate varies inversely as its length and directly as the square root of its elasticity, and therefore, in the case of stretched membranes, directly as the square root of the extending force, just as in the case of an extended string. In the case of membranous tongues, a third influence must be added, viz. that of the violence of the impinging blast of air, which has no effect upon the pitch of notes caused by the vibration of the usual firm tongue. The note is not simply intensified by increasing the strength of the blast, but its pitch is raised (J. Müller). This is explained by the consideration that the tension of the membrane is also at the same time increased ; for the middle position about which the tongue vibrates deviates further from the position of rest with a strong than with a weak blast ; and this greater deviation increases the tension of membranous tongues, as is evident, while it does not affect the elasticity of firm plates, in so far as that property is concerned in the vibrations. The law of this increase in pitch as the blast becomes stronger has not yet been determined. The form and size of the slit only affects the note to the extent that, with the same expenditure of energy, the narrower the slit the greater the accu-

mulation of air behind the tongue, the greater the pressure upon the latter, and, in consequence, the stronger the blast it is possible to obtain.

If the tongue is fixed into a pipe (reed-pipe) that portion of it which conveys air to the tongue is called the wind-pipe, while that which is beyond the tongue is called the sound-pipe. In general the effect of the sound-pipe may be said to be to add its own proper tone to the sound produced by the vibrating tongue, and to intensify certain of the component tones of the latter. By intensifying one of the harmonics the pitch of the resulting sound is apparently raised, as the intensified tone becomes prominent as the principal tone. On the contrary, if the primary tone of the sound-pipe is deeper than that produced by the tongue, an apparent diminution of pitch may result. The sound-pipe of the vocal organ has this effect only to a slight extent, the timbre, or sound-colour, of the voice being but slightly, though clearly, modified by it (see below, Vowels), and the principal tone of the sound produced in the larynx remaining the same.

The Larynx.

In the larynx the membranous tongue is formed by two horizontal membranous plates, the *inferior vocal cords*, which extend between the inner surface of the thyroid cartilage and the anterior and external surfaces of the arytænoid cartilages, and are covered by the laryngeal mucous membrane, which is here provided with pavement epithelium. The slit between them (glottis vocalis) is continuous posteriorly with the interspace between the interior surfaces of the two arytænoid cartilages (glottis respiratoria). The thyroid and arytænoid cartilages are so fixed to the cricoid cartilage as to admit of a certain degree of movement. The former, the thyroid cartilage, turns about a horizontal transverse axis in such a manner that its anterior portion approaches or recedes from the anterior portion of the cricoid. The effect of this movement is to increase or diminish the angle of inclination of the thyroid with the vertical, and, in consequence, to move its superior portion, to which the vocal cords are affixed, forwards or backwards. The arytænoid cartilages turn principally about their long vertical axes, the effect of which is, as they are pyramids with triangular bases, to cause their edges to occupy different positions, and thus to alter the shape of the slit. From what has been just said it is clear that the thyroid cartilage influences, especially by its position, the length and tension of the vocal cords. The thyroid cartilage may therefore, with regard to the vocal cords, be fitly styled the 'cartilage of ex-

tension,' the cricoid the 'basement cartilage,' and the arytænoid the 'cartilage of position' (Ludwig).

The following are the muscles which govern the relative positions of those cartilages with which the vocal cords are connected :

1. The *crico-thyroidei* approximate the thyroid to the cricoid cartilage, rotating the former about its axis in a forward and downward direction, and thus pulling the upper portion of the cartilage forward, and extending the vocal cords when the arytænoid cartilages are firmly fixed.

2. The *thyro-arytænoidei*, which run for the most part within the vocal cords, rotate the thyroid cartilage in a direction upwards and backwards towards the arytænoid cartilages, and therefore render less tense the vocal cords. Some of their fibres arise from points of the vocal cords themselves, and must therefore, on contraction, confer different degrees of tension upon different parts of the vocal cord ; for only that portion will be rendered lax in which the contracting fibres run, while the rest will be kept tense. As, moreover, a portion of the fibres are attached about the external edge of the arytænoid cartilage, the effect of contraction must be to press together the anterior internal edges (processus vocales) of the opposing cartilages, and to separate their posterior internal edges, the result being that the glottis vocalis is narrowed to a small slit, while the glottis respiratoria is increased to a triangular space.

3. The *crico-arytænoidei postici* drag the external edges of the arytænoid cartilages, to the lower extremities of which (processus musculares) they are attached, backwards and downwards, thus at the same time rotating outwards the anterior internal edges (processus vocales), separating them slightly above, and approximating the posterior edges. The effect of this movement is to convert both the glottis vocalis and the glottis respiratoria into triangular spaces, which together form a wide rhombic aperture.

4. The *crico-arytænoidei laterales* drag the muscular processes of the arytænoid cartilages downwards, forwards, and outwards, whereby the apices of the two pyramids are somewhat separated one from the other, while the bodies of the latter are so rotated as to occupy the position they take up on contraction of the thyro-arytænoidei muscles, with the exception that

the processus vocales are not so closely applied one to the other.

5. *Arytænoidei proprii* (inter-arytænoidei, transversus et obliqui) approximate the apices of the pyramids and their posterior edges one to the other. If they act in concert with the thyro-arytænoid muscles, both glottis vocalis and glottis respiratoria are closed, and respiration completely interrupted, as, *e.g.* immediately before coughing.

The ventricles of Morgagni give the vocal cords free space in which to vibrate, a provision especially necessary when the vocal cords are much arched by the strength of the impinging blast of air. The superior vocal cords do not appear to play any part in the production of voice. It has certainly been observed that a diminution in the calibre of the sound-pipe above the tongue of a reed instrument raises the pitch of the note produced (J. Müller); but experiment has shown that the excised larynx constantly gives the same note whether the upper vocal cords be present or not. In birds the vocal cords are not, as a rule, concerned in the production of notes, the latter being the function of the 'inferior larynx,' a characteristic organ situated in the majority of cases at the point of division of the trachea.

The larynx receives its supply of motor nerves from the inferior laryngeal branch of the vagus, paralysis of which occasions loss of voice. The superior laryngeal branch of the vagus is considered to supply the crico-thyroid muscle only; but this is denied by some authorities (Nawratil).

Sounds produced by the Vocal Organs.

The general conditions necessary for the production and alteration of sounds will easily be perceived from what has already been said concerning reeds and reed-pipes. In general there is necessary a blast of air of a certain strength, the production of which requires the closure of the glottis respiratoria and the narrowing of the glottis vocalis. These actions are effected by the contraction of the crico-arytænoidei laterales or of the thyro-arytænoidei. During the contraction of the crico-arytænoidei postici the production of voice is impossible. From what has been said above, it is moreover evident that the pitch of the note sounded depends upon the length and tension of the vocal cords, and upon the strength of the blast. It is, on the contrary, independent of the shape of the glottis, which only varies in accordance with the strength of the blast, being narrower in the production of a stronger blast. The pitch is also independent of the form and length of the wind-pipe and sound-pipe in the case of the larynx. It may therefore be

stated that the pitch of the note rises: 1. With increasing tension of the vocal cords, which is induced (*a*) by the contraction of the crico-thyroidei (perceptible externally to the touch); (*b*) by the relaxation of the whole of the thyro-arytænoidei ; (*c*) by increased violence of blast (p. 304) of which use is chiefly made in the production of the highest notes, which can therefore only be rendered *forte* and not *piano*. In order to produce the strongest blast of air through the larynx, the glottis vocalis must be made as narrow as possible, and the glottis respiratoria completely closed, the latter action being effected by the arytænoidei proprii. On the contrary, the tenser the vocal cords the stronger must be the blast of air necessary to cause them to vibrate ; and, in consequence, the greater must be the atmospheric pressure in the trachea, as may be proved by means of a manometer fixed into a tracheal fistula (Cagniard-Latour). The pitch of the note also rises (2) according as the length of the portion of the vocal cord set vibrating diminishes. The latter is brought about without at the same time disturbing the tension, (*a*) by partial contraction of the thyro-arytænoidei (p. 306); (*b*) by the close apposition of the processus vocales of the arytænoid cartilages, whereby the portions of the vocal cords in which the cartilages are placed are prevented from vibrating ; (*c*) in larynges of small dimensions, especially in those of women and children, the general range of pitch is higher on account of the shortness of the cords. All the above statements are based upon observations which have, in addition, taught us that as the pitch of the note increases the superior vocal cords approach nearer and nearer to one another without ever completely closing the orifice between them, and that the epiglottis falls more and more over the opening into the larynx (Garcia). Moreover, as the pitch increases the larynx rises, owing partly to the contraction of the elevators of the larynx, and partly, in all probability, to the extension of the trachea under the increasing pressure of the air within. In spite of the apparent simplicity of the arrangements, the process of the production of voice must be extremely complicated. For example, with a given arrangement of the vocal cords any increase in the force of the blast not only intensifies the note, but also raises it ; as, however, we may require to sustain the same note with a varying intensity (*piano* and *forte*), in order to do so a

continual process of compensation must be kept up by the muscles.

In conducting observations on the production of voice in the larynx the following methods are practicable : 1. Palpation and auscultation of the larynx from without. 2. Direct observation of the interior of the larynx by means of a laryngoscope (Garcia, Czermak, Türck). The latter instrument consists of a small mirror, which is held, by means of a handle, at an angle of 45°, over the opening of the larynx and in front of the velum palati, having been previously warmed to prevent the condensation of vapour upon it. Concentrated light is thrown upon this small mirror by means of another concave mirror provided with an aperture to which the eye of the observer is applied. The mouth of the patient is opened wide and the tongue pulled forward. By the arrangement of mirrors the top of the larynx is seen strongly illuminated. 3. Observation of the larynx of a living animal exposed from above. 4. Experiments with the excised larynges of human bodies (J. Müller). The action of the muscles is imitated by passing threads to which weights are hung over pulleys, and attaching them to the points of insertion of the muscles they are to represent, pulleys and larynx being fixed to a stand. The blast of air is transmitted through a tube fastened into the trachea either from the lungs of the experimenter or from a pair of bellows. In order to measure the pressure of the air in the trachea, a manometer is connected laterally with the tube, which is continuous with the trachea. To study the effect of the sound-pipe, the larynx is left attached to the head. Experiments with the larynges of dead subjects have led to many results inconsistent with the appearances of the living larynx, some of which are still unexplained, and which indicate our lack of knowledge respecting the actions of the latter. 5. Experiments with artificial larynges (J. Müller) ; to this class of experiments belong, generally, all experiments with reed-pipes.

A greater height of pitch than can be attained by the ordinary method of production of voice is possible by means of the so-called 'falsetto voice.' This is another register, another method of producing voice, which is specially suitable for the higher notes, and which differs from the usual method in a manner which is not yet thoroughly understood. Besides the superior pitch of the 'falsetto notes,' they differ essentially in timbre or tone-colour from those ordinarily produced. It has been observed that the glottis vocalis during the emission of falsetto notes is wider than in the formation of the ordinary voice ; and that the superior vocal cords are also farther apart. It is further maintained that the true vocal cords do not vibrate in such an extent of their breadth (in fact only at their edges) in the former case as in the latter (J. Müller, Lehfeldt),

owing, according to Mandl, to the partial imposition upon them of the superior vocal cords. Others state exactly the reverse of this, viz. that a greater breadth of the vocal cords is in vibration during the utterance of falsetto notes (Garcia). It is, finally, probable that an extreme tension of the vocal cords is necessary for their production, as is indicated by the sense of exertion in the larynx under those circumstances. Owing to the greater width of the glottis vocalis during the use of falsetto, the air in the lungs is quickly exhausted, in consequence of which it is impossible to sustain a falsetto note as long as an ordinary one. Another distinction between notes of the two registers, and one which depends upon the circumstance last mentioned, originates in the resonance of the wind-pipe and sound-pipe in the two cases; this will be referred to below.

As was said previously, the form and length of the wind- and sound-pipes have no influence in the case of the larynx upon the pitch of the notes. They serve, however, to intensify them, and also to modify them, inasmuch as the tones to which they gave origin intensify certain of the harmonics of the voice, and so regulate the timbre, which forms such an essential distinction in the voices of different individuals. By means of voluntary alterations in the form of the sound-pipe the latter may be made to give rise to special tones and noises which are essential to speech (see below). Owing to the accumulation of mucus, &c. in various parts of the windpipe, or about the vocal cords themselves, other noises may be produced, which are unnecessary, or even detrimental to perfect speech. In the production of ordinary voice, resonance is strongest in the windpipe, as it contains the air which is being compressed through the narrow slit of the glottis vocalis. The bronchial tubes and the parietes of the chest therefore enter strongly into resonance, and give rise to a trembling motion (fremitus pectoralis). Hence, ordinary full and powerful voice is called 'chest-voice.' In the production of falsetto notes, on the contrary, no resonance of the chest takes place, owing to the greater width of the glottis vocalis, the sound-pipe, and the cavities of the nose and mouth being the chief seats of resonance.

The compass of the chest-voice when the vocal organs are

fully developed, ranges from about two to two and a half octaves; but the limits vary with the size of the larynx. The general range of voice is lowest in men and highest in women and children. Thus the bass as a rule extends from E (80 vibrations per second) to f' (342); the tenor from c (128) to c'' (512); the alto from f (171) to f'' (684); and the soprano from c' (256) to c''' (1024). The complete compass, therefore, of the human voice ranges from about E (80 vibrations per second) to c''' (1024 vibrations per second), nearly four octaves. The range from c' (256) to f' (342) is common to all voices; but the character of the notes varies in different individuals, according to the timbre or 'colour' they acquire from the larynx. In many cases the limits here set down are exceeded.

The development of the larynx bears a definite relationship to that of the sexual powers. At the commencement of puberty there is a sudden increase in its size, and the alto or soprano (treble-voice) of the boy changes into the bass or tenor of the man. This is what is commonly known as the 'breaking' of the voice. In castrated individuals, and in cases of hypospadias, &c., the voice remains abnormally high, higher even than the soprano of women.

2. Speech.

Speech consists of certain tones and sounds which the expired air produces in the cavities above the larynx, and which are used for the purposes of speech, either alone—as in whispering—or in conjunction with the sounds of the voice—as in speaking aloud.

The elements, the sequent arrangement of which constitutes speech, are called *articulate sounds*, and are divided into *vowels* and *consonants*. The distinction, which was formerly described as existing between these two classes, viz. that the consonants are those articulate sounds which cannot be uttered without the aid of vowels, cannot now be held. Both consonants and vowels are now regarded as being capable of utterance alone, if we except that certain of the former lose somewhat of their characteristics (see below). The true distinction between them is, that the consonants are indefinable sounds, while vowels have rather the character of tones. That is to say, when whispered, the latter are sounds produced in the

cavity of the mouth, in which a tone predominates whose pitch may be determined, and when spoken aloud they are modifications of the voice caused by the intensification of individual harmonics by the 'proper' tone of the buccal cavity at the time.

Vowels.

1. In whispering, vowels are produced by expelling a current of air through the cavity of the mouth, the shape of the latter being different for each vowel. Sounds are thus produced in which, by a careful examination, and especially on comparing the various vowels, tones of definite pitch may be distinguished. For the same vowels the same tones are found to be remarkably constant in persons of varying age and sex; and they may be determined by means of the piano (Donders). These tones are the characteristic tones of the cavity through which the current of air passes. They may be still better determined by means of resonators in the following manner. Tuning-forks are set vibrating, and successively placed in front of the mouth, which is arranged as if for the production of a certain vowel; as soon as a tuning-fork is thus placed, the prime tone of which is in unison with that of he buccal cavity, the tone emitted is intensified by resonance, and rendered more audible (Helmholtz). The form of the cavity of the mouth during the production of the vowel sounds U [1] and O, is that of a globular flask with a short neck; during the production of A, that of a funnel with the wide extremity directed forward; of E and I, that of a globular flask with a long narrow neck, &c. Corresponding with the characteristic tones of such bodies, the tones of the cavity of the mouth are:—

for U—f
„ O—b'
„ A—b''
„ E—f and b''' ⎱ one tone for the body of the
„ I—f (?) and d'''' ⎰ flask, the other for the neck

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[1] The vowel-sounds referred to here are those of the German language:

a like a in *father*
e „ e „ hen
i „ i „ *fi*sh
o „ o „ *o*pen
u „ oo „ *ooze*

(Helmholtz). Slight modifications of pronunciation materially affect the tone. The constant occurrence of the same characteristic tone for the same vowel in buccal cavities of different sizes is accounted for by the proportionate alteration in the orifice of the mouth.

According to more recent researches (König) the characteristic tones of the various vowels are :

for U—b
„ O—b'
„ A—b''
„ E—b'''
„ I—b''''

The various forms of the buccal cavity are brought about in the following manner. In the production of all the vowels, if the buccal cavity alone is to be used the passage of the current of air to the nasal cavities is prevented by the raising of the soft palate. If this is not done the vowels have, when spoken aloud, a 'nasal' character. This elevation of the soft palate is least complete during the production of A, becoming more and more so in the case of the other vowels in the following order: E, O, U, I. The various flask-like arrangements of the mouth are thus produced : in A the cavity of the mouth is largest, owing to the position of the tongue along the floor, the mouth being wide-open (funnel-shaped). In O and U the globular flask is produced by the elevation of the root of the tongue, and the contraction of the aperture of the mouth into a round opening which is narrower in the case of U than of O. In E, I, the long neck of the flask is produced by approximating the tongue to the hard palate, &c. In sounding all the vowels except U the larynx moves upwards somewhat, least of all in the case of O, and more so in the cases of the others in the following order, A, E, I.

2. In speaking aloud, vowels result from the intensification of various of the harmonics of the voice by means of the resonance of the buccal cavity (Wheatstone, Helmholtz). Hence it follows that vowels may be best sung with those notes which have a prominent harmonic agreeing with the 'proper' tone of the cavity of the mouth; further, that the individual vowel-sounds are not distinguished by the peculiar arrangement of the intensified harmonics, but by their absolute height.

The vowel-sounds may easily be analysed by means of the resonance-apparatus mentioned on p. 303. The analysis is more exact if made by means of a phonautograph (Donders), in which a tense membrane is allowed to take up the vibrations of a particular vowel-sound and to trace them upon a rotating cylinder. In order to reproduce a vowel-sound synthetically, all that is necessary is to raise the damper from the strings of a piano and to sing the vowel in a clear, loud voice in front of the instrument. Under such circumstances all the strings the tones of which exist in the vowel-sound as harmonics, are called into vibration (p. 302), and to a degree of intensity corresponding with the intensity of the harmonics. The vowel, therefore, *resounds* from the instrument, not simply as a tone, but as a vowel (Helmholtz). The direct synthesis out of simple tones is still more instructive. A number of tuning-forks corresponding in pitch with the various harmonics of a primary tone (*e.g.* B, *b*, *f′*, *b′*, *d″*, *f″*, *as″*, *b″*, *d‴*, *as‴*, *f‴*, *b‴*) are set vibrating by means of electro-magnets, which are so arranged that the current passing round them is opened and closed by the vibrations of a special tuning-fork fitted up on the principle of Wagner's hammer. The tones of the tuning-forks are rendered inaudible by placing them upon caoutchouc. Before each fork, however, stands a resonance-tube tuned to the prime tone of the fork. When the tube is open, it renders audible the prime tone of the tuning-fork,—a simple tone, therefore. With this apparatus it is possible, by opening the resonance tube more or less perfectly by means of keys, to sound and combine at will strong or weak individual tones. In this way not only vowels, but also the characteristic sounds of various instruments, may be synthetically represented. The same result may more simply be effected by means of reed-pipes, which yield simple tones (Helmholtz).

Diphthongs are produced during the transition from the form of mouth necessary for the one vowel to that necessary for the other. They consist of two sounds following quickly one upon the other.

Consonants.

The articulate sounds called consonants are sounds produced by the vibrations of certain easily movable portions of the throat and mouth; and they have a different sound according as they are accompanied by voice or not. The pharyngo-buccal canal is capable of constriction or interruption at three places, at each of which vibrations may be produced; these are: 1. At the lips, the constriction being formed by the two lips, or by the upper (or lower) lip with the lower (or upper) row of teeth. 2. Between the tongue and the palate, the constriction being brought about by the apposition of the tip of the tongue to the anterior portion of the hard palate, or the posterior sur-

face of the upper row of teeth. 3. At the fauces, the constriction being due to the approximation of the root of the tongue and the soft palate. Sounds may originate at each of these places of interruption; and hence consonants may be classified into three series, viz. labial, dental, and guttural consonants.

The sounds which may be formed at each of the places of interruption are (Brücke):

1. EXPLOSIVES. These are produced by suddenly opening or closing the passage at one of the points mentioned during the expulsion of air: *a*, without the aid of voice, P, T, K; *b*, with the aid of voice, B, D, G.

Opening of the passage is necessary for the formation of one of these consonants when it begins a syllable; closure when it ends one (e.g. *pa*, *ap*). As P, T, and K are distinguishable from B, D, and G respectively only by the absence or presence of the voice, no sharp distinction is possible between them during whispering.

2. ASPIRATES. The passage is constricted at one of the above-mentioned points to a small slit through which the current of expired (or inspired) air can rush. Hence arise the following consonants: *a*, without the aid of voice, F, S (sharp), Ch (guttural); *b*, with the aid of voice, V, Z, J (as in the German *ja*, &c.). At the constriction between the tongue and the palate a second aspirate may be formed, in addition to the sharp S, viz. L, by completely closing the passage in front and allowing the air to escape only at the sides between the molar teeth. By forcing air through two narrow spaces situated one behind the other, viz. that between the tip of the tongue and the hard palate, and that between the two rows of teeth, two other sounds may be produced: *a*, without the aid of the voice, Sh; *b*, with the aid of the voice, Zh. If a space be left between the tip of the tongue and both rows of teeth, the following consonant-sounds are produced: *a*, without the aid of the voice, Th (hard) as in *than*; with the aid of the voice, Th (soft) as in *thunder*. The guttural Ch may be produced near the front of the mouth as in the German word, *ich*; or near the back, as in *ach*.

F and V, &c. are distinguished in the same way as P and B, &c.

3. RESONANTS. The current of air no longer passes through the usual opening, which is closed, but through the nose, which

is left open by the depending soft palate. The aid of the voice is necessary. The consonants thus produced are M, N.

4. VIBRATORY SOUNDS. There are three varieties of the vibratory R which differ in their place of origin. The first is the labial R, produced by the vibration of the lips, which does not occur as an articulate sound in any European language; the second is that produced by the vibration of the tip of the tongue in the constricted portion of the buccal cavity formed by the tongue and the teeth; and the third is the guttural R. In order to produce them the pharyngo-buccal cavity is constricted at the necessary point, but not firmly; and the margins are then set vibrating by the expiration of air. The vibrations are, however, too slow to give forth a definite note.

The consonants may therefore be grouped in the following manner :

	Labials	Dentals	Gutturals
1. Explosives :			
a. Without the voice	P	T	K
b. With the voice	B	D	G
2. Aspirates :			
a. Without the voice	F	S (hard), L, Sh, Th (hard)	Ch (in 'ich' and 'ach')
b. With the voice	V	Z, L, Zh, Th (soft)	J (in 'ja')
3. Resonants	M	N	N (nasal)
4. Vibratory sounds	Labial R	Lingual R	Guttural R

H is the sound produced in the larynx by the quick rushing of the current of air through the widely-opened glottis.

Compound consonants are produced by suddenly opening the air-passage previously closed for the utterance of P, T, or K, as the case might be, and allowing the current of air to rush through the second of the before-mentioned places of constriction narrowed as if for the utterance of S (hard) : thus are produced Ps (Greek Ψ), Ts (German Z), and Ks (X). Other compound consonants are formed by the rapid transition from the position of mouth necessary to produce one consonant to that necessary to produce the other.

Observations upon the movements which take place during the formation of speech are made partly by direct inspection of the cavity of the mouth while the latter is open, and partly by palpation by means of the fingers

introduced into the mouth. In order to decide whether the posterior nares are opened or closed at any particular time, a candle-flame, or a bright, cold mirror may be placed in front of the nasal openings on the face. Finally, many of the conditions of speech have been determined by noticing the mode of utterance in persons suffering from pathological malformations of the vocal organs; such as absence, or adhesions of the soft palate, &c.

PART III.

THE LIBERATING APPARATUS.

The·Nervous System.

WE have already broadly described in the Introduction (p. 5 *et seq.*) the arrangement of the liberating apparatus (the nervous system), and its relationships, on the one hand, to the external world, and on the other, to the 'organs of work.' From what was there said, it will be seen that the following five groups of organs are to be distinguished in the nervous system :

1. Organs by means of which energy is set free in the organs of
   • work—viz. the nervous end-organs in parenchymatous tissues, glands and muscles.
2. Organs which transmit the process of liberation from the central nervous organs to those included under group 1— viz. the centrifugal conducting apparatus.
3. Central nervous organs.
4. Organs which transmit the process of liberation originating from the external medium, to the central nervous organs—viz. the centripetal conducting apparatus.
5. Organs upon which the movements of the external medium first act in order to set in action.the processes of liberation which it is the function of the fourth group of organs to transmit—viz. the organs of sense.

For physiological purposes, however, this fivefold division of the nervous system is unnecessary. The centrifugal and centripetal conducting apparatus are undistinguishable one from the other in their characters, and differ only in being connected peripherally with organs which are different (see groups 1 and 5).

We must therefore distinguish: apparatus for conduction; central-organs; sense-organs; and end-organs situated in the organs of work. The two last-mentioned sets of apparatus may, also, both be regarded as peripheral end-organs of the conducting apparatus, as is done in Chap. X.

CHAPTER IX.

THE CONDUCTING APPARATUS (NERVES).

A. GENERAL PHYSIOLOGY OF NERVES.

THE elements of a nervous cord are thin, longitudinally striated, fibres, which are arranged side by side into round or flattened bundles (*nerves*), and bound together, like the 'muscle tubes' of muscle, by means of interspersed connective tissue which extends over the exterior of the bundle as a firm fibrous sheath (*perineurium*). Each nerve-fibre is a tube filled with partly fluid contents. The thin walls of the tube (the primitive sheath, *neurilemma*) consist, as in the sarcolemma of muscles, of an elastic membrane, and are provided with large nuclei. The contents of the tubes are divided into a thin cord running in the axis—*the axis-cylinder*—and a shining mass surrounding it—*the medulla or medullary sheath*—composed of a substance which easily breaks up.

The fine nerve-fibres of a certain class do not possess a medullary sheath, and consist simply of an axis-cylinder and a sheath (*non-medullated nerve-fibres*). A third class of nerve-fibres is characterized by the regular varicose arrangement of the axis-cylinder, and the absence of all signs of a sheath (*gray or varicose fibres; fibres of Remak*).

The distribution of the various classes of nerve-fibres will be discussed in Chap. XI.

The axis-cylinder is especially well seen after the death of the nerve; and it has therefore been considered by many to be a post-mortem contracted coagulum. The greater number of observers, however, regard it as existing during life; and, indeed, it must be considered to be the most important element of the nerve-tube, as it is connected directly with the essential portions of the central and peripheral nervous end-organs, unless we are prepared to regard the latter also as the appearances of coagulation. Many

axis-cylinders, if not all, consist of a bundle of very fine ' nervous fibrillæ ' (Max Schultze). An especially delicate species of axis-cylinders (simple nerve-fibrillæ, Max Schultze) is discovered in the central nervous organs, forming there intercentral connections between the ganglion-cells (Chap. XI.) ; the thickness of a nerve-fibre depends essentially upon the greater or less thickness of the medullary sheath, which seems to serve the purpose of nourishing the axis-cylinder. Under certain methods of treatment medullated nerve-fibres exhibit at definite distances apart annular constrictions at which the medullary sheath is said to be interrupted. As a nucleus of the neurilemma is constantly found between two such constrictions, it would seem as if the appearances were indications of the original formation of a nerve-fibre out of a row of cells, the constrictions corresponding with the divisions between the primitive cells (Ranvier).

Chemical Constituents of Nerves.

Scarcely anything is known about the chemical constitution of nerves. The axis-cylinder seems to be related in its characters to the albuminous bodies. The medullary sheath, whose appearance and behaviour towards solvents indicate a fatty nature, possibly contains no proper fat, but only lecithin and protagon (pp. 21 and 36). These, however, have only been prepared hitherto from brain-substance, &c., and not from nerve-fibres themselves. Nerve-fibres contain in addition cholestrin and creatine.

The reaction of fresh nerve in a state of rest is neutral (Funke). The reaction and composition of brain-substance will be discussed in Chap. XI.

The Various Conditions under which Nerves exist.

Nerves, like muscles, may exist in three conditions: 1. The usual condition of Rest. 2. The condition of Death. 3. The condition of Activity. The three conditions cannot, however, in the case of nerves, be distinguished by mere inspection, as the physical properties of the nerves undergo no alteration.

The mere mechanical properties of nerves have, as a rule, no interest physiologically speaking. Flaccid nerves have a tendency to form fine transverse folds—the transverse striæ of Fontana.

Nerves in a State of Rest.

A certain amount of material exchange occurs in nerves in a state of repose, just as was seen to be the case in muscles, although hitherto neither absorption of oxygen nor formation

of carbonic acid has been proved to take place. The existence
of such processes may, however, be inferred from the fact that
nerves contain specific tissue-elements which differ from the
constituents of the blood. The extent of the material exchanges
occurring in nerves must be very slight, as nerves are almost
destitute of blood-vessels; but nothing more particular is known
about them.

Nerves in a State of Death.

The death of nerve-tissue is not marked, like that of muscle,
by any evident process of coagulation; it is only recognized by
the loss of irritability (see below), the appearance of an acid
reaction (Funke), and the electro-motor phenomena which will
be described hereafter. Dead nerve-tissue undergoes putrefac-
tion, just like dead muscle, if not prevented from doing so by
a process of drying.

Nerves in a State of Activity.

The active condition is induced in nerves by the same
means as in muscles, viz. by some liberating force—some
stimulus; and the term 'irritability' is applied to nerves as
to muscles, to indicate this property of being called into
activity by the application of a stimulus.

The conditions of irritability and the stimuli, in the case
of nerves, agree in many particulars with those of muscles.
The irritability of nerves is greater than that of muscles; that
is to say, stimuli which are physically equal (*e.g.* equal degrees
of variation in electric currents which are of the same inten-
sity), have a more powerful stimulating effect when acting
upon muscle through a nerve, than when acting directly upon
a muscle deprived of its nervous connections by the action of
curare (Rosenthal).

Irritability.

Irritability is connected with the normal constitution of
nerves. As, however, our knowledge of the latter is very
superficial, it must suffice to establish empirically the condi-
tions which increase, diminish, or destroy irritability. In the

majority of cases the rationale is unknown. The following are the facts connected with this question :—

1. When a nerve ceases to be connected with a living central organ, owing, for example, to section of the nerve or death of the central organ, its irritability increases considerably at first, but afterwards diminishes and finally disappears. Transverse section of the nerve hastens the process (Rosenthal); which, moreover, takes place more quickly in the central portions of the nerve than in those nearer the periphery (Ritter and Valli's law). A nerve separated from its central organ, but still allowed to remain in the body, subsequently undergoes certain chemical and morphological changes, denominated 'fatty degeneration.' If, however, the cut ends be kept in apposition, they grow together after some time. The presence of oxygen is as little necessary to the maintenance of irritability in the case of excised nerves as in that of muscles (Pflüger and Ewald, p. 243).

2. Continued repose of a nerve diminishes and destroys its irritability, and leads at last to fatty degeneration. Sensory nerves, when cut across, undergo degeneration in both their central and peripheral portions—in the former because they can no longer be irritated, in the latter because they are separated from the central nervous organ.

3. Continued activity of a nerve diminishes its irritability in proportion to the time, and may destroy it altogether (Exhaustion). In the former case rest restores the nerve to its original condition. The alterations which take place in nerves during exhaustion have not yet been made out.

4. Any decided mechanical alteration in the condition of a nerve, such as tearing or twisting, destroys its irritability.

5. Any decided disturbance of chemical composition, such as desiccation, treatment with strong alkalies or acids, etc., has the same effect.

6. The effects of temperature, hitherto studied only on frogs, are the following. Temperatures above 45° C. destroy irritability, the more rapidly the higher they are, the destruction being instantaneous at 70°. If the temperature to which the nerve has been subjected have not exceeded

50°, irritability may be restored on cooling (Rosenthal). Below 45°, a rise in temperature at first increases, but afterwards diminishes, irritability, the increase being greater and the diminution more rapid according as the temperature is higher. Rise in temperature, therefore, diminishes the duration, while it increases the intensity, of irritability (Afanasieff). A sudden rise of temperature to 35°–45° acts as a stimulus (see below).

7. The effects of electrical currents through nerves appear to be especially important. If a constant galvanic current be passed through a portion of a nerve, its whole length enters into an altered condition (du Bois-Reymond), in which, among other circumstances, its power of being stimulated is modified (Eckhard, Pflüger). This is called the ' *electrotonic* ' condition, or ' *electrotonus* ' (du Bois-Reymond). The condition which obtains in the region of the positive electrode (the *Anode*) is called '.anelectrotonus,' and that in the region of the negative electrode (the *Cathode*), ' *catelectrotonus* ' (Pflüger). The constant current which causes this change of condition is called the ' *polarising* ' or ' *electrotonising* ' current. The boundary between the anelectrotonic and catelectrotonic states, called the ' *indifferent point* ' of the ' intrapolar region,' is situated near to the anode when the polarising current is weak, and moves towards the cathode as the polarising current increases in strength. The influence of electrotonus is strongest in the neighbourhood of the pole. Irritability is *increased* in the *catelectrotonic area* and *diminished* in the *anelectrotonic area.* Immediately after the cessation of the polarising current the conditions of irritability become reversed in the different regions (irritability being increased near the anode and diminished near the cathode); but afterwards they gradually regain the normal (Pflüger). At the instant of closure of the current, irritability is said to be increased in the whole nerve (Wundt). (Reference should be made in this connection to what is said below about Stimuli and the Electrical Phenomena of Nerves.)

The variations of irritability may be explained, for the sake of illustration, by supposing for the moment that the particles of nerve-matter in

the anelectrotonic area have a diminished, while those in the catelectrotonic area have an increased, degree of mobility. Variations in irritability are measured either by differences in the degree of contraction produced by stimuli which should be weak ; or by variations in the strength of the stimulus, which is just sufficient to induce the slightest contraction. The results so obtained admit of an explanation, to be mentioned below, which does not require the assumption of variation in the degree of irritability.

The electrotonic variations of irritability may be demonstrated in the case of man also by the application of a constant current (Eulenburg, Erb). To prevent disappointment, however, the test-stimulus must be applied at the points where the current is most dense, as it is only in the immediate neighbourhood of the electrodes that the current passed through the nerve is dense enough to induce the phenomena of electrotonus ; and hence it is that it appears as if there were an anode on each side of the cathode, and a cathode on each side of the anode (Erb).

Stimuli.

The stimuli which are able to call a nerve into activity are the following :—

1. *Variations in an electrical current.*—A completely constant current flowing through a nerve does not appear to be essentially capable of stimulating the nerve to activity even if apparently so. Every variation, on the contrary, in the intensity of the current (or, more exactly, in the density[1] of the current) produces irritation in the nerve, which is more powerful the more quickly or suddenly the variation occurs (du Bois-Reymond). The variation which is most frequently used as a stimulus is that produced on making or breaking a current through the nerve : *i.e.* the passage of the intensity from nothing to the full strength of which the current is capable, or the reverse. Any other variation, however, acts as a stimulus ; *e.g.* the sudden increase or diminution in strength of a current already passing through the nerve ; or the mere alteration of the density of the current in a nerve, the intensity of the whole current remaining unaltered.[2]

---

[1] By the density of a current is understood the intensity of the current divided by the area of transverse section of the body through which it is flowing—in this case, of the nerve. The value is clearly relative, for the same intensity of current must have more marked effects the thinner the nerve.

[2] The latter is effected by suddenly laying over the nerve, through which a current is passing, a moist conductor. The current which had previously to traverse the nerve alone in order to complete its circuit, now passes through both conductors, the effect of which is to diminish suddenly the density of the current in the nerve.

If the time occupied by one complete variation be supposed to be divided up into fractions, and these fractions taken as abscissæ ; and if the density of current corresponding with each of those fractions of time be regarded as ordinates ; a curve will be obtained which will represent the course of the variation according to time. From the law just enunciated of the stimulation of nerves by currents, it follows that the value of a given variation as a stimulus is greater the more sudden the ascent or descent of this curve ; but the more exact conditions of this relation are at present unknown. From the same law we gather that a nerve may be very powerfully stimulated by means of a very weak current, if only the rapidity with which it is allowed to break into or out of the nerve be sufficiently great. Hence the shocks of frictional electricity have a very powerful stimulating effect ; for although the amount of electricity really present is very small, the currents it forms are extremely rapid in their appearance and disappearance. For similar reasons, the rapid currents of the induction coil are generally used for the purposes of stimulation. On the other hand, it is evident that a very strong current may be made to pass through a nerve without inducing irritation, if care be taken to do it extremely gradually.

The above-mentioned stimulation by *constant* currents is evidenced in the case of motor nerves by the induction of tetanus in the muscle with which they are connected, and in the case of sensory nerves by sensations (pain, &c.), which continue during the passage of the current. The appearances in the former case are more marked with ascending than with descending currents. They are present in the case of very weak currents, and become more and more decided as the current increases in strength, until a certain limit is reached, above which the electrotonic modifications of the conditions of irritability again render the results less marked (Pflüger).

The stimulating effect of a current operates, on closing (and, in general, on any *positive* variation), at the *cathode* only ; and, on opening (*negative* variation), at the *anode* only. In other words, *a portion of nerve is stimulated by a current, when the latter causes in it the appearance* (or *increase*) of *catelectrotonus*, or the *disappearance* (or *diminution*) of *anelectrotonus* (Pflüger). The stimulation of the other portions of the nerve is only a consequence of the transmission of irritation (see below).

Expressed in the hypothetical manner made use of on p. 325, Pflüger's law of stimulation would run thus : The passage of the molecules of nerve-matter from the usual into the mobile (catelectrotonic) condition ; or from the hardly mobile (anelectrotonic) into the usual condition, acts as a stimulus. On the contrary, the passage from the usual into the hardly mobile (anelectrotonic) condition ; or from the easily mobile (catelectrotonic) into the usual condition, does not act as a stimulus. In this form the law is somewhat more intelligible, on account of the rationale supplied.

The experiments from which this law has been deduced are rather compli-

cated. As they have been for the most part made upon motor nerves, the law is also called the 'Law of Contraction.' If the stimulating current be allowed to pass through a given (central) portion of the nerve, the whole of the latter is divided into two parts, in which opposite conditions obtain, in one the *anelectrotonic,* in the other the *catelectrotonic.* The above law affirms that, on closing the stimulating current, it is the catelectrotonic area only, while, on opening, it is the anelectrotonic area only, which suffers stimulation. Hence we may, if we like, express the law as follows: *Stimulation proceeds from the cathode on closing, and from the anode on opening, the stimulating current.* If the stimulating current has an *ascending* direction (*i.e.* if the positive electrode is nearer the muscle) it is evident that the upper portion of the nerve will be stimulated during closure, and the lower during opening, of the stimulating current: and the contrary results will obtain if the current is *descending.* It may now be asked, which regions of the nerve, on stimulation, call the connected muscle into activity, *i.e.* induce contraction; and the answer will be found to depend upon the strength of the current used in stimulation. Thus, when the current is strong, the anelectrotonic area loses its powers of conductivity (see below), in consequence of which only the stimuli operating in the portion of nerve between it and the muscle can possibly produce a contraction. In the case of strong currents, therefore, the *descending* current can only act effectively on closing and the *ascending* only on opening. With currents of medium strength both areas or regions have the power of inducing stimulation and causing contraction of the connected muscle, as the conductivity of the whole nerve is nowhere interrupted. In this case, therefore, whatever the direction of the current, contraction will follow on both opening and closing. With currents of the weakest sort, that area only will act as a stimulus in inducing contraction which is most favourably situated for the purposes of stimulation; that is to say, *cæteris paribus,* that area which is most removed from the muscle (see under Conductivity). When, therefore, the current is very weak, closing the ascending, and opening the descending, current should induce contraction. But, as the appearance of catelectrotonus is a stronger stimulus than the disappearance of anelectrotonus, the latter operation, viz. opening the descending current, gives place to closure of the same as a more powerful means of stimulation; and, in consequence, the weakest descending currents do not give opening—but closing—contractions. The law of contraction may be formulated thus:

(R = Rest, C = Contraction).

Strength of current	Ascending		Descending	
	On closing	On opening	On closing	On opening
Strong . . .	R	C	C	R
Moderate . .	C	C	C	C
Weak . . .	C	R	C	R

Induction currents are currents which are called into existence very suddenly and disappear somewhat more slowly. Of the two means of stimulation which follow thus immediately one upon the other, the former, according to the above-mentioned general law of stimulation, is the more powerful. In the case of weak currents, indeed, it is the only one of the two which is effectual; so that weak induction currents act in stimulation like the closure of a similarly directed constant current. With this understanding, the Law of Contraction holds for induction-currents also (Rosenthal).

The effects of stimuli on the centripetal nerves of animals can only be imperfectly investigated. The method adopted is to induce an extreme reflex irritability by means of strychnia-poisoning, in order that peripheral stimuli may readily induce tetanic muscular contractions (Chap. XI.). An analogous law of stimulation may be demonstrated in the case of inhibitory nerves, as, for example, the inhibitory fibres of the vagus (Donders).

If the current used in stimulation is very strong, or has been kept closed for some time, tetanus occurs on opening (tetanus of Ritter), instead of the usual single contraction. This tetanus immediately disappears on reclosing the same current, but is, on the contrary, intensified if the current is first reversed and then closed. As Ritter's tetanus results from the strong irritating effect due to the disappearance of anelectrotonus, it ceases immediately on separating the anelectrotonic area of the nerve from the muscle; which can only be done, for obvious reasons, in the case of descending currents, where section of the nerve at the 'indifferent point' (p. 325) accomplishes the purpose (Pflüger). The condition of the nerves just referred to was formerly considered to be a distinct modification of irritability, similar to those described on p. 325; and it used to be said that the constant current increased the irritability of the nerve for the opening of a current in the same and for the closure of a current in the contrary direction; and *vice versâ* (Rosenthal). The phenomena described are, however, easily explicable by Pflüger's law of stimulation. If the stimulating current is too weak, or has been closed for an insufficient time; or if the irritability of the nerve is diminishing on account of the approaching death of the latter; a somewhat languid contraction takes place, followed finally by the usual opening contraction, instead of the tetanus of Ritter.

The power of constant currents to restore irritability to exhausted muscles, to which reference was made on p. 249, also belongs to this category of phenomena; for it must not be forgotten, that all the laws of the electrical stimulation of nerves are equally applicable to muscles. In the case of muscles also, for instance, stimulation only results on opening a current in the same, or on closing a current in the contrary direction.

As stimulation, according to Pflüger's law, depends upon the appearance or disappearance of a different condition (electrotonus) of the nerve, none can result from currents which are

too transitory to allow of the completion of the electrotonic state. Experiment confirms this statement; as currents which do not last more than 0·0015 of a second are incapable of stimulating nerves (König).

Currents have the most powerfully stimulating effects when they traverse the nerves in the direction of their length, being indeed powerless in this respect when flowing transversely. Currents in directions intermediate between these two extreme positions have intermediate values as stimuli, the laws of which have not yet been established. The length of the portion of nerve traversed by the stimulating current, which was formerly supposed to influence irritability favourably, is now known to do so only in the case of descending currents, while in ascending currents the shorter the piece of nerve included between the electrodes, the better appears to be the stimulating effect. Stimulation, therefore, according to the law of electrotonus, is more powerful the nearer the cathode to, and the farther the anode from, the muscle (Willy).

In the electrical stimulation of muscles, the same laws hold as in that of nerves (p. 248). Here, also, it is only variations in currents that produce stimulation, which, as before, proceeds, on closing, from the cathode, and, on opening, from the anode (von Bezold). As changes take place more slowly in muscle than in nerve (as evidenced, for example, by the different degrees of rapidity with which they transmit impressions), length of duration of the stimulating current is more necessary in the former than in the latter for the production of stimulation. Hence all induction-currents, and the more transitory constant currents are unable to stimulate to contraction muscle deprived of its nervous connections by curare, while they are able to cause contractions in a muscle by acting upon its motor nerves (Brücke). This fact was early known to be the case with muscles, the nervous organs of which were rendered incapable of performing their functions by exhaustion, local death, pathological paralysis, &c. (von Bezold, Fick, Neumann).

Pflüger's law of stimulation may be demonstrated to hold in the case of muscles in the following ways (Engelmann):

1. A muscle A B (Fig. 9) is fixed by its middle portion c, care being taken not to crush it, and the lower half is arranged so as to register its

contractions on a myographion. If the cathode be placed at A and the anode at B, the latent period (p. 257) occurs sooner during a closing contraction than during an opening contraction, as in the former case the stimulus proceeds from A and in the latter from B; and *vice versâ.*
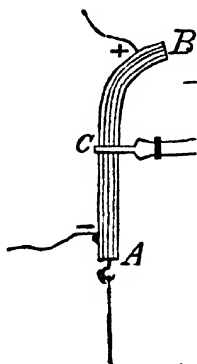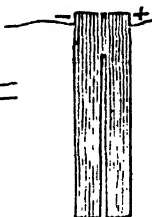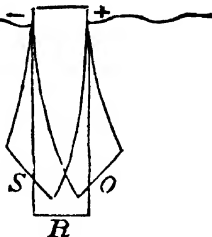
FIG. 9.   FIG. 10.   FIG. 11.

2. If the electrodes be placed at the thin edges of a piece of flat muscle, split as in Fig. 10, contraction follows, on the passage of a moderate current, in the strip next the cathode on closing, and in that next the anode on opening; of course each fibre has its own cathode and anode, but the density of the current is only sufficient to induce contraction in the neighbourhood of the points where stimulation originates. If the muscle be not split (Fig. 11) it bends, for the same reasons, on closure towards the cathode (s) and on opening towards the anode (o).

2. *Chemical stimuli.*—It may be stated in general[1] that whatever effects in a nerve a change of chemical constitution of a certain extent and with a certain degree of rapidity acts upon it as a stimulus. Almost all chemical stimuli cause at the same time the death of the nerve to which they are applied, *i.e.* they destroy its irritability. But the contrary of this cannot be stated, viz., that all destructive substances act as stimuli; for some of them, as, for instance, ammonia and solutions of metallic salts, produce death so rapidly as to prevent the development of the stimulating effect. Chemical stimuli must, as a rule, be in a more concentrated state for nerves than for muscles, as the substance of the former, especially the sheath, permits but slow diffusion of liquids. The principal chemical stimuli for nerves are the following (Eckhard, Kühne): concentrated solutions of the mineral acids, alkalies, alkaline salts, concentrated lactic acid, concentrated glycerin, &c. Deprivation of water (desiccation) also acts as a strong stimulus.

3. *Thermal stimuli.*—A temperature of from 34° to 45°C. acts as a stimulus upon the motor nerves of the frog, without producing serious consequences ; temperatures up to 40° causing clonic, and temperatures above 40° tetanic, contractions of the connected muscles. Higher temperatures (p. 324) kill the nerve without acting as stimuli (Rosenthal, Afanasieff).

4. *Mechanical stimuli.*—All mechanical impressions which cause alterations of form in any portion of a nerve with a certain degree of rapidity (*e.g.* blows, pressure, ligature, section, &c.) act as stimuli while producing the change. If the form of the nerve has been permanently injured, irritability and conductivity are, as a rule, lost.

5. *Natural stimuli* originating in the end-organs ; that is to say, the stimuli induced in the central nervous organs, or in the special nervous terminations of the organs of sense by the action of light, sound, heat, pressure, &c., which it is the function of the nerves to conduct (consult the Introduction to this Section ; and also Chaps. X. and XI.).

Phenomena of the Active Condition.

Concerning the active condition of the nerve itself, very little is as yet known. We know neither the nature of the forces which become free during that condition nor the chemical processes which form their basis. There is absolutely no indication in the case of nerves—such, for instance, as exists in the shortening of muscle—which serves to distinguish an active from an inactive portion ; and the only chemical difference which has been insisted upon between nerves which have been at rest and nerves which have been in activity, is (Funke, J. Ranke), that the latter exhibit an acid reaction ; but even this is denied by other observers (Liebreich, Heidenhain). As little is known about the utilisation of oxygen by active nerves as by inactive nerves. No generation of heat can be shown to take place in active nerves (Helmholtz, Heidenhain). More will be said concerning the electrical appearances and the temporary duration of the activity of nerves when considering their electromotor properties.

Transmission of the State of Activity along the Nerve-fibres. (*Conduction.*)

The state of activity in a nerve, which, as above mentioned, is accompanied by no external manifestations, leads to change in one of its two end-organs, the peripheral or the central. Under ordinary circumstances, the stimulus, which throws the nerve into the active state, is applied to one of these end-organs, whereupon a certain change, which we are accustomed briefly to call the ' result,' becomes evident in the other. If this ' result ' occurs in the central end-organ after stimulation applied to the peripheral, the process is called *centripetal* ; and if the contrary, *centrifugal.*

As a rule, only one of these directions is possible in particular nerve fibres ; hence a distinction is made between centripetal and centrifugal nerves and nerve fibres. In addition to this natural method, in which the stimuli are applied to the end-organs, nerves may be artificially stimulated at any point in their course ; but in this case also the result takes place in the same way as on natural stimulation, viz. in a central organ in the case of a centripetal fibre, and in a peripheral organ in the case of a centrifugal fibre.

The simplest explanation of this behaviour is that which supposes that on normal stimulation of an end-organ the whole course of the nerve is not thrown into the active condition at once, but that the state of activity is transmitted from one cross section to the next, and so conducted through the whole course of the nerve ; that, moreover, any stimulus applied at any point in the course of a nerve-fibre induces the active condition at that point only, whence it is transmitted to the next point, and so on, just as in the case of normal stimulation. This property which nerves have of transmitting the active state from one point to the next until the end-organ is reached is called their *conductivity.* The condition necessary for conduction is that, between the stimulated point and the end-organ in which the result is to be manifest, the nerve be quite intact. Lesion at any point in its course through section, pressure (ligature), burning or chemical destruction (treatment with caustics), interrupts conduction. In addition, the other

circumstances which diminish irritability act at the same time prejudicially upon conductivity, as, for instance, the anelectrotonic state. The passage of the active condition from one fibre to another never occurs.

Such a passage seems to take place in the case when, on isolated electrical stimulation of one branch of a nerve, contractions follow in a muscle supplied by another branch. This so-called 'paradoxical contraction' will be discussed more at length in treating of the electrical phenomena.

In order to explain the difference between a centripetal and a centrifugal nerve-fibre, it was formerly supposed that every nerve had the power of conducting in one direction only, the former towards the central, the latter towards the peripheral, nervous organs. Such a supposition is, however, unnecessary, as every nerve is connected with one end-organ only which is capable of exhibiting the results of conduction. For example, no nerve exists which is at one end connected with sensory ganglion-cells and at the other with a muscle, in which, therefore, conduction in both directions might be proved. Hence there is no necessity of a specific distinction between centripetal and centrifugal nerves; and we may suppose that all nerves can conduct in both directions, but that only one of the end-organs of each is capable of indicating that conduction. That such a conductivity in two directions does really exist seems to be indicated by the following circumstances : 1. If a nerve be stimulated at a given point, the electrical changes characteristic of nervous activity appear, not on one, but on both sides of the point of stimulation (du Bois-Reymond). 2. If one terminal twig of a forked motor nerve be stimulated, activity is induced in the other terminal twig, provided the common trunk be intact. The fibres of the former twig must, therefore, have conducted in a centripetal, and not in their usual centifugal direction (Kühne). 3. No anatomical, chemical, or physiological distinction has hitherto been made out between fibres of the two classes. 4. The most direct proof, however, of this power of nerves to conduct in opposite directions is an experimental one. If the central portion of a severed sensory nerve be caused to unite with the peripheral portion of a divided motor nerve, an arrangement will have been created for indicating conduction in two directions (Bidder). This experiment has

been performed in the case of the peripheral part of the hypoglossus and the central part of the lingualis; and the results were such as were anticipated (Philippeaux and Vulpian, Rosenthal).

A physiological distinction between the two classes of nerve fibres has been sought in the statement that certain poisons affect one kind only; thus it is said, for instance, that the arrow-poison, curare, paralyses motor nerves alone (p. 247). It has, however, been shown that the action is one upon peripheral end-organs, and therefore does not affect the properties of the nerves themselves.

The active condition, therefore, induced first of all at the spot where the stimulus was applied, is transmitted by conduction to the regions on both sides of the spot in the case of a stimulus applied at an intermediate point of the nerve-fibre; or to the region on one side only in the case of a stimulus applied to an end-organ. By this means every portion of the nerve passes successively into the state of activity. It has been observed (Pflüger) that the effect of stimulation, as manifested in an end-organ (*e.g.* the contraction of a muscle on irritation of a motor-nerve) is more marked the farther removed is the point of stimulation from the end-organ. This is explained by supposing that the condition of activity does not travel along a nerve with unaltered force, but that it increases like the momentum of a falling mass ('cascade-' or 'avalanche-effect'). It is, however, more probable that this phenomenon depends upon an increased irritability of the more distant portions of the nerve due to artificial division where such has taken place, or, perhaps, in other cases, to the proximity of the central organ with which it is connected.

Rapidity of Conduction.

The processes of transmission, upon which conduction depends, take up a definite time. Conduction therefore takes place with a certain, and not very great, degree of rapidity. For the motor nerves of the frog, this rapidity is about 26–27 metres per second (Helmholtz). For the sensory nerves of man the determinations vary. The following are some of the principal results of experiments:

94 metres per second	.	.	.	.	.	(Kohlrausch)
60	„	.	.	.	.	(Helmholtz)
34	„	.	.	.	.	(Hirsch)
30	„	.	.	.	.	(Schelske)
26	„	.	.	.	.	(de Jaager)
41·3	„	.	.	.	.	(von Wittich)

For the motor nerves of man, the mean rapidity is about 33·9 metres per second (Helmholtz and Baxt), which is, doubtless, the correct rate for sensory nerves also. Rapidity of conduction is modified by various influences, being diminished, for instance, by cold (Helmholtz), and also by either phase of the electrotonic condition (von Bezold). It is, moreover, probable that rapidity of conduction is not uniform, but diminishes as the distance from the place of origin of the stimulation increases (H. Munke, Helmholtz and Baxt).

For the determination of the rapidity of conduction in the motor nerves of the frog the same method is made use of as in the discovery of the time taken up in muscular contraction (p. 258). That is to say, the same nerve is successively stimulated at two different points in its course (*a* and *b* in Fig. 5); on stimulation of a point nearer the muscle the period of latent contraction is of shorter duration than on stimulation of a point more distant, in consequence of which contraction of the muscle occurs more quickly. The duration of the latent period in each case may be registered either by Pouillet's method or by means of the myographion; and the difference of duration taken in connection with the measured distance between the two points of stimulation gives the data for determining the required rapidity of conduction in the nerve (Helmholtz).

In the case of man, physiologists were formerly limited, in the determination of the rapidity of conduction, to sensory nerves. The general method of procedure is as follows: The person experimented upon gave, on perceiving a certain sensation, a preconcerted signal. The time intervening between this signal and another connected with the stimulus which had given rise to the sensation was measured by means of one of the numerous instruments devised for such a purpose. Sometimes Pouillet's method was made use of. Hipp's chronoscope (for an account of which, see the Text-Books of Physics) was another instrument used; as was also Krille's registering apparatus, in which marks were made upon a rotating cylinder, while a pendulum was so arranged as to record seconds on the cylinder at the same time. In Hankel's registering apparatus, which was also used for this purpose, the marks coincident with stimulation and sensation were made by the pressure of a pencil upon a surface of paraffin fixed at the circumference of a quickly revolving wheel, while the rate of rotation of the wheel was checked by means of Krille's instrument. Another instrument was König's phonautograph, on the same principle as Krille's, except that a vibrating tuning-fork recorded time instead of a pendulum; the object of

this improvement being to register much smaller intervals than is possible with a pendulum, a most important point when the rate of rotation varies. The time—so measured—is divisible into three portions : *a* the time taken up by the passage of the sensation to the brain; *b* the time occupied in the perception of sensation and the origination of motor impulse; *c* the time which elapses from that origination to the occurrence of the pre-arranged signal; that is to say, T = *a* + *b* + *c*. If now the experiment be twice made, once with a stimulus applied at a point near the brain, and once at a point more remote (say at the neck and at the foot respectively), the difference between the two times T and T′, considered in relation with the difference in length of the nerve traversed, would give the desired rapidity of conduction ; supposing always that the difference between T and T′ consists of that between *a* and *a*′ only, and that *b* and *c* remain the same in both experiments. The latter supposition, however, with regard to *b*, cannot always be relied upon as holding ; for it has been found that the kind of sensation, a previous knowledge or ignorance of it, the expectation of it at a given time, the character of the pre-arranged signals, &c., have the greatest influence upon the time (Donders and de Jaager). The great difference observable in the determinations of various observers may, therefore, depend either upon the inconstancy of the factor *b* or upon real individual differences of conductive power.

The rate of conduction of motor nerves of man is determined by tracing upon a myograph the curve of contraction of the muscles of the thumb by means of their increase in thickness (p. 259). Two tracings must be taken, one when the stimulus has been applied to the nerve at a point on the arm near to the hand, and the other when it has been applied at a point more remote from the hand, from which the determination is easily made (Helmholtz). It may be mentioned, by the way, that weak stimuli were found during these experiments to be conducted more slowly than strong ones.

Electrical Phenomena of Nerves.

1. *Action of Galvanic Currents upon Nerves.*

The resistence of nerves to electrical conduction is about five times as great in a direction across, as in the direction of, the fibres : in dying, this difference is diminished by about one-half. The cause of this condition is altogether or in part an internal polarization, which appears at the border between the sheath and contents of the nerve-tube. This polarization develops instantly on closing, and vanishes as suddenly on opening, the current in the course of which the nerve is placed. Similar phenomena are noticed in the case of muscles in which the resistance in a transverse direction is seven times as great as that in a longitudinal direction (Hermann).

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During electrotonus a current having the same direction as the polarizing current is everywhere demonstrable in the extra-polar region, and adds itself algebraically to the current of repose, where such is present. This electrotonic current is strongest in the region of the electrodes. It appears immediately on closing, and is constantly diminishing on the side of the cathode (du Bois-Reymond).

No current in the same direction as the polarizing current is known to exist in the intra-polar region, in addition to the polarizing current itself (Hermann).

The sudden appearance of the electrotonic current in the extra-polar regions may act as a stimulus upon neighbouring nerves, thus causing 'secondary contraction or secondary tetanus' (p. 275); of such a nature is the 'paradoxical contraction,' already mentioned, which follows in a muscle connected with one branch of a nerve after the electrical stimulation of another branch of the same nerve : it is explained by supposing that the contiguity of the fibres of the two branches gives opportunity for the sudden appearance of the electrotonic current in the one to act as a stimulus upon the other (du Bois-Reymond).

After breaking the polarizing current certain 'after-currents' remain (Fick) for a short time. In the intra-polar and anelectrotonised extra-polar regions they have the opposite direction to the polarizing current; but in the catelectrotonised extra-polar region the 'after-current' has the same direction as the polarizing current (Hermann).

The electromotive force of electrotonic currents is very great. Some electrotonic currents have been observed to possess electromotive force equal to half that of a Daniell's element (du Bois-Reymond).

2. *Essential Electrical Properties of Nerves.*

In a portion of nerve bounded by two transverse sections, the existence of currents is demonstrable which obey the same laws as those of muscle (du Bois-Reymond, p. 270 *et sq.*).

No currents have with certainty been detected at any natural cross-section of a nerve.

The electromotive force of the current passing from longitudinal to transverse sections of a nerve is, as a rule, equal to about ·02 of that of a Daniell's element (du Bois-Reymond).

On stimulation of a nerve the electromotive force of the essential nerve-current is diminished (du Bois-Reymond). This 'negative variation' which, if the stimulus is strong enough, may proceed to the reversal of the nerve-current, develops

more quickly than it disappears, and occupies altogether about ·0007 of a second (Bernstein). In polarized nerves the extra-polar electrotonic currents also exhibit a 'negative variation' on stimulation (Bernstein); in the intra-polar region stimulation induces the appearance of an accessory current in the same direction as the polarizing current (Hermann).

Stimulation applied to a nerve-trunk is evidenced by the negative variation of its proper current just as a stimulation of intramuscular nerve-terminations is evidenced by muscular contraction. The same use may, therefore, be made of negative variation, as of the contraction of muscle, for the discovery of the laws of stimulation of nerves. Both, for example, are diminished if the region of stimulation be already anelectronised, and increased if it be catelectrotonised (Bernstein); and the interval of time between stimulation and the occurrence of the negative variation may be used, in the same way as the interval between stimulation and contraction, in determining the rapidity of conduction (Bernstein). Since the difficulty is great of arranging nerves (p. 334) so as that both ends shall be connected with muscles, whilst it is easy to have a nerve with two artificial transverse sections, negative variation affords the simplest means of proof of the power of nerves to conduct in opposite directions (du Bois-Reymond).

It is, moreover, necessary, just as in the case of muscle (p. 275), to apply to nerves a considerable number of rapidly succeeding stimuli in order to indicate the negative variation of their currents by the needle of a multiplier. It is not possible, as a rule, to get evidence of negative variation by means of the physiological rheoscope, as 'secondary contraction and secondary tetanus' proceeding from nerves are not caused by the negative variation of the proper currents of the latter, but by the currents due to electrotonus. For example, 'secondary contraction' does not follow at all when the stimulus applied to the nerve is not electrical; and it may be shown by means of the Law of Contraction that, under certain circumstances, 'secondary contraction' depends upon a stimulation of the rheoscopic nerve due to a *positive* variation, such, *e.g.*, as that caused by the appearance or disappearance of electrotonus (du Bois-Reymond). The following experiment serves for determining the length of time which elapses between stimulation and the occurrence of negative variation (Bernstein): A quickly revolving wheel causes at each revolution, (1) the electrical stimulation of a point, *a*, of the nerve, and immediately afterwards (2) the transitory closure of a circuit which includes a galvanometer and a portion of nerve *b*, arranged as for the demonstration of its natural current. The interval of time between (1) and (2) can be varied at will; and, by gradually increasing it from 0, a point is at last reached at which closure of the galvanometer-circuit exactly coincides with the commencement in the region *b* of the negative variation due to the stimulation of *a*. The time thus determined clearly indicates the period required for the irritation to travel from *a* to *b*. This period is proportional to the length of nerve between *a* and *h* (whence it immediately follows that the effect of stimulation commences

the moment it is applied) ; and from the data it has been calculated that irritation travels at the rate of 28·718 metres per second.

If the time between (1) and (2) be so arranged that the nerve-current in *b* shows, at the moment of closure of the galvanometer-circuit, not the beginning but some other phase of the negative variation, say the maximum, or the end, it is possible to determine from the time intervening between (1) and (2) the duration and progress in time of the negative variation itself.

There are two theories regarding the currents of nerves as of muscles (p. 276 *et sq.*). According to one (du Bois-Reymond) every nerve-fibre contains regularly arranged electromotive molecules, which present their positive elements to a longitudinal, and their negative elements to a transverse, section, and whose activity diminishes on stimulation. Electrotonic currents are explained, according to this hypothesis, by attributing to the polarizing current a directive action upon the movable molecules, which are supposed to be so turned as to have the same direction as the polarizer. In order that this should be possible, each molecule must be supposed to be divided into two bipolar halves, incapable of mechanical or chemical separation, each of which can, however, rotate about an axis of its own. By this means an arrangement of the halved molecules end to end is possible, which is most complete in the neighbourhood of the polarizing electrodes, and which explains the electrotonic current.

In opposition to this explanation of electrotonic currents may be cited the condition of the intrapolar region. According to the above theory this region should exhibit an extremely powerful accessory current in the same direction as the polarizer, whereas there is no trace of such a current.

The other theory (Hermann) explains the natural current of nerves, like that of muscles (p. 277), as the effect of contact: the contents of nerve-tubes which are dying or in activity are negative to the contents of nerve-tubes which are living and at rest. The cause of the electrotonic phenomena is the polarization at the boundary between nerve-sheath and contents to which reference has already been made.

If a current passes from one conductor to another, and if at the boundary between them polarization, and, in consequence, resistance take place, both current and state of polarization spread out over the region about the points of entrance and exit. In consequence of this any pair of electrodes situated in an extra-polar region receives a branch of the current having the same

direction as the polarizing current. In the intra-polar region the branches of the original current would be found, if it were possible to demonstrate them, to have a direction opposite to that of the polarizer. This circumstance, which was first shown to occur in the case of moist, covered wires (Matteucci), is taken to explain electrotonus in nerves, as in the latter the necessary conditions are present (Hermann). The polarization-currents remain a short time after the polarizer is broken; but in the anelectrotonic area the more powerful effect of the opening or breaking shock at the anode produces the appearance of reversal of the after-current, which flows in an opposite direction to the polarizer (see above).

If, as was supposed on page 332, conduction in a nerve is nothing but the transmission of the condition of activity from one portion to another, then both the above theories of the nerve-current must require that, while a nerve is conducting, the point of it at which the active condition for the moment obtains must be negative towards every other point in the long axis of the nerve. No direct indication of such a condition has as yet been given.

The alterations of electrotonic currents effected by stimulation may be explained by assuming that irritation in its course through the polarized nerve varies in intensity, increasing when it reaches a point which is more positive (*i.e.* which is more strongly positively, or more weakly negatively, polarized), and diminishing when it reaches a point which is more negative. In this way are explained : 1. The positive increase of current in the intra-polar region ; for irritation is more powerful as it reaches the anode than as it reaches the cathode, and in consequence the former becomes through irritation more strongly negative than the latter. 2. Similarly the diminution in extra-polar electrotonus. 3. The negative variation of the proper nerve-current ; for the latter causes negative polarization in the neighbourhood of the transverse section, in consequence of which irritation is less powerful by the time it has reached the transverse section, and every longitudinal section therefore becomes on irritation more strongly negative than a transverse section. It follows on the contrary from the same supposition that any irritation arising in a positively polarized (anelectrotonic) portion of nerve must diminish in its course through the nerve, while any irritation arising in a negatively polarized (catelectrotonic) portion must increase. Hence we can see the cause of the apparent diminution of irritability

which occurs during anelectrotonus, and of the apparent increase during catelectrotonus (and in the neighbourhood of the transverse section). The phenomena described on page 325 may also in this way be explained (Hermann).

Theories concerning the Nature of Nervous Activity.

Most thinkers on the subject assume the existence in nerves of movable or alterable particles, so connected together that the movement or alteration of any one leads to the movement or alteration of those in its immediate neighbourhood. Many identify these particles with those which are assumed for the purpose of explaining the electromotive properties (p. 340) of nerves. It is further supposed that the movement or alteration of which the particles are capable, takes place in opposition to resistances or inhibitions whose power is inversely proportional to the irritability of the nerve. These inhibitions or resistances are diminished in catelectrotonus and increased in anelectrotonus.

The motion or alteration of one of the nerve-particles would, therefore, act like a stimulus on the next, whereby it seems to be implied that conductivity proceeds *pari passu* with irritability. The latter is not apparently always the case. Thus, in the catelectrotonic condition, irritability is increased while the rapidity of conduction diminishes (pp. 325 and 336); in the spinal cord there are said to exist conducting fibres which are incapable of direct stimulation (Chap. XI.); and nerves poisoned by conine, curare, or carbonic acid, as well as, occasionally, the nerves of paralysed parts, are said to be still able to conduct irritations from the nervous centres, but are incapable of direct stimulation (Schiff, Erb, Grünhagen).

There are various views as to the nature of the process of stimulation. Some are inclined to imagine a real movement (rotation, deviation, &c.), others a chemical change, a decomposition analogous to that which takes place in muscle, and which sets free a similar process in neighbouring particles somewhat as fire travels along a train of gunpowder. This decomposition would occur slowly even during repose and would be accelerated by death and the influences increasing irritability. Stimuli (influences suddenly working) would cause great acceleration and the impulse to decomposition would be imparted to the neighbouring particles the more quickly according as the rapidity of the process was greater. Death spreads slowly, and irritation quickly, through nerves, the latter the more quickly according as it is stronger.

Polarization which occurs at the border between the sheath and contents of a nerve-tube and upon which electrotonus depends (p. 340) possibly plays an important rôle in the transmission of irritation. As, for instance, a stimu-

lated portion of the interior of a nerve is electrically negative to the surrounding portions which have not been stimulated, small currents arise which tend to equalise through the sheathing substance. They have, however, the effect of producing anelectrotonus, and therefore of inhibiting irritation at the point of stimulation, and of causing catelectrotonus, with the accompanying irritation, in the surrounding non-stimulated portions.

The Function and Classification of Nerve Fibres.

Although it is highly probable that all nerve-fibres are alike (p. 334), some classification of them is expedient. The usual division is founded upon the accidental function of the fibres' as indicated by the arrangement of their end-organs. The function of a nerve thus determined is called its ' specific energy.' All nerve-fibres, or, more exactly, all nerve-fibres with their accompanying end-organs, may, therefore, be divided into :

A. *Centrifugally conducting fibres* (p. 333) : 1. Motor fibres, at the peripheral end of which is a muscular fibre or another of the contractile elements mentioned in the preceding Chapter ; 2. Secreting fibres, at the peripheral extremity of which stands a glandular element, and whose specific energy consists in stimulating increased secretion in glands, without the aid of the vaso-motor apparatus, on reflex or central excitation ; 3. Trophic fibres, *i.e.* such as regulate the processes of nutrition (oxidation) in the various parenchymata, and therefore have the same relation to the parenchymatous juices as secreting fibres to free secretions. Their existence, although not improbable, has never yet been demonstrated. Almost all the phenomena which have hitherto been cited to prove their existence may be referred to the action of motor (and especially vaso-motor), secreting and even sensory fibres, as will be stated in describing the trigeminal nerve. The only undoubted case of nervous influence on nutrition is that of the influence on the nutrition of nerves themselves. It has been previously stated that divided nerves undergo fatty degeneration in their peripheral portions.

The secreting nerves, and the trophic nerves if they exist, also influence the formation of heat (pp. 5 and 96), and might, therefore, be described as thermal, just as muscular nerves are described as motor. The influence of nerves upon local tem-

peratures appears, however, to be connected with the distribution of blood (vaso-motor nerves, compare p. 227).

B. *Centripetally conducting fibres* :—1. Sensory fibres. the central end-organ of which is an organ of the mind, and the result of irritation of which is a mental operation, viz. sensation ; their peripheral end-organs are organs of sense (Chap. X.) ; 2. Reflex, or excito-motor, fibres, in the central end-organ of which the irritation which has traversed the fibre to that point is transferred to another fibre and finally to a centrifugal system.

The central organs connected with the sensory fibres have to do with various kinds of sensations, some with sensation of sight, others with sensations of hearing, &c.   The same sensory fibre always calls into action the same portion of the mental apparatus, and always therefore produces the same sort of sensation, in whatever way it is stimulated.   Hence, the ' specific energy ' of the optic fibres is the transmission of visual impressions, that of the acoustic fibres the transmission of auditory impressions, &c.   Further, it is necessary to ascribe to the irritation of different fibres the different qualities of any given sensation, e.g. the sensation of red and of blue light, or of high and of low notes, and hence, to suppose that certain fibres have, as their ' specific energy,' to aid in the perception of the red rays, while that of others is to assist in the perception of the blue.   For, if it were not so, we should be compelled to assume that one and the same nerve-fibre was capable of states of irritation which were qualitatively different —an assumption hitherto entirely unsupported by facts.   There must, therefore, be at least as many sensory fibres as simple qualities of sensation, and the student may be reminded that the innumerable varieties and shades of sensation which are actually experienced arise from the mingling in various ways of a relatively small number of simpler qualities (Chap. X.). Although this logical consequence of the principle of specific energy (Young, Helmholtz) is a physiological postulate, it is as yet only applicable to a few of the organs of sense.

This principle is apparently at variance with our experience that the nerves of taste occasion different sensations, according as they are stimulated by ascending or descending currents. The experiments in question, however, admit of another explanation (Chap. X.).

The peripheral end-organ of every sensory nerve (organ of sense),—and such organ alone—is capable of excitation not only by the stimuli common to all nerves, but also by one peculiar to itself, which constitutes its usual means of irritation. Thus the end-organs of the optic fibres in the retina are irritable by means of waves of light; those of the acoustic fibres by waves of sound; those of the olfactory fibres under the influence of odorous bodies, &c.

As the mind has no means of recognising the origin of any given stimulation, it assumes that all sensations come from their usual source. For example: (1.) It refers the origin of every sensation which reaches it through a sensory fibre to the end-organ of that fibre, even though stimulation has not been applied in the usual manner but to the trunk of the nerve. Thus, persons who have had a limb amputated feel sensations caused by any irritation of the stump of the nerve as if they arose in the amputated limb (eccentric reference of sensations.) (2.) In the case of special sensations it assumes the stimulus to have been that which usually causes the same sensation (light, sound, &c.), notwithstanding that any of the common nervous stimuli (mechanical, electrical, thermal or chemical) may have originated it. Thus it considers every visual sensation as occasioned by waves of light which have impinged upon the retina, even though mechanical disturbance of the retina, pressure on the optic nerve, &c. may have been the cause. The conclusions arrived at by the mind concerning the origin of stimulation go in many cases still further, as, for example, when the stimulus proper to a given organ of sense always takes the same path in order to reach it. Thus, it supposes every wave of light impinging upon the retina, or every wave of sound acting upon the acoustic nerve, to have previously traversed the transparent media of the eye, or the conductors of sound of the ear, as the case may be. Hence, it refers the causes of all sensations of light or sound to without. In the case of visual sensations the mind even forms a judgment as to the *position* of the illuminating body, or at least as to its direction. In the act of seeing, every illuminated point of the retina may be connected with the point whence the rays of light proceed by means of the axial ray of the particular pencil illuminating that point (Chap. X.), and the

cause of the visual sensation is referred to the external medium in the direction of this ray even though that cause be subjective.

C. *Intercentral fibres*; that is to say, such as unite two central organs (ganglion-cells). Their number is enormous, and their function, which is as yet only hypothetical, will be discussed in Chapter XI. The following are included under this head : the majority of the fibres of the brain and spinal cord ; the chief portion of the sympathetic nerves ; the so-called inhibitory nerves ; &c.

B. SPECIAL PHYSIOLOGY OF NERVES.

The various nervous fibres, motor, sensory, &c., are so arranged as a rule that all those destined for the same region of the body, of whatever sort they are, run together for a certain distance in one ' mixed ' nerve-trunk, which gives off branches composed of one kind of fibres only (' sensory nerves,' ' motor nerves ') when the locality about to be supplied by those branches is almost reached. In the case of cranial nerves, the whole course of which is short, this union is rarely if ever effected. Cranial nerves are, therefore, from their origin for the most part either purely motor or purely sensory.

The object of the special physiology of nerves is to determine for each nerve-fibre its specific energy, which is called for the sake of brevity its ' function.' This would be self-apparent in the case of any fibre, if its two end-organs were anatomically known and their functions understood. Here the two sciences of anatomy and physiology mutually supplement one another.

In order to determine the special function of a nerve the following methods are adopted :

1. A nerve is divided at any point. Stimulation applied to the nerve on that side of the point of section remote from the organ in which the results of excitation would follow normally no longer produces the customary results. Thus, if it is a muscular nerve which has been divided, the muscles connected with it remain inactive although the will, or a reflex or automatic stimulus, or any other excitant applied to the nerve above the place of section, are still operative,— the muscle is ' paralysed ; ' while, if the nerve is centripetal, stimulation of the sense-organ, or excitation of the peripheral portion of the nerve, no longer induces sensations, and blindness, deafness, insensibility, &c. follow.

2. The ends of the nerve on each side of the place of section are irritated respectively, for the most part with tetanic stimuli, and the consequences noticed.

Nerve-trunks are divided according to their origins (their central ends) into Cranial, Spinal and Sympathetic Nerves.

I. Cranial Nerves.

For greater detail concerning the origin of the cranial nerves refer to Chap XI.

First pair (Olfactory nerve).—The fibres of this nerve have the function of conducting every irritation, at whatever point of their course it originates, to that portion of the brain concerned in the sensation of smell, thereby giving rise to that sensation. Irritation always takes place physiologically in the peripheral end-organs situated in the olfactory membrane of the nose (Chap. X.), by means of specific irritants, 'odorous bodies.' Section of the olfactory bulb, which is practicable in the case of young animals, destroys the sense of smell (Biffi).

The production of the sensation of smell on stimulation of the olfactory nerves by means of ordinary nerve-stimulants, has not yet been directly demonstrated.

Second pair (Optic nerve).—All stimulations of this nerve cause irritation of that portion of the brain concerned in the perception of light, and, in consequence, produce the impression of luminosity. Its normal stimulus proceeds from the peripheral terminations of its fibres in the retina of the eye. It has, in addition, the power of calling into reflex action the sphincter of the iris through fibres of the motor oculi proceeding to that muscle. The optic chiasma is discussed in Chap. X.

Third pair (Motores oculi).—This nerve is the motor nerve for most of the orbital muscles, viz. for the rectus sup., rectus inf., rectus int., obliquus inf., and levator palpebræ superioris ; for the circular muscle of the pupil and the tensor choroideæ. It may be called into activity by voluntary stimuli, or those of its fibres destined for the iris may be excited in a reflex manner by irritation of the optic nerve (Chap. X.). It is maintained by some that it contains also sensory fibres ; but it seems probable that it does not possess any until after its

union with the trigeminal nerve; this is, however, denied by Adamük.

Section and paralysis of the motor oculi causes: 1. Drooping of the upper eyelid ('ptosis'). 2. Rotation outwards of the eyeball, since the muscles supplied by it can no longer balance those supplied by the fourth (trochlearis) and sixth (abducens). 3. Dilatation and insensibility to light of the pupil. 4. A constant state of accommodation for long distances.

In animals, the fibres for the pupil are said occasionally to run in the abducens instead of in the motorius oculi (Adamük). In their course to the iris they traverse the ciliary ganglion and nerves.

Fourth pair (Trochlear, or pathetic).—This is the motor nerve for the obliquus superior muscle of the eyeball. The existence of sensory fibres in this nerve is maintained by some writers.

Fifth pair (Trigeminal).—This is a mixed nerve, arising, after the fashion of a spinal nerve, by two roots, a sensory (large) and a motor (small), and soon afterwards splitting up again into motor and sensory branches. The sensory root, like the sensory root of a spinal nerve, possesses a ganglion—the Gasserian or semilunar ganglion.

Its *sensory* fibres confer sensibility on nearly the whole of the head, and they serve the purposes of a large number of reflex acts. The regions of the head not supplied by the trigeminus are: portions of the pharynx, palate and root of the tongue which receive branches from the vagus and glosso-pharyngeus; the Eustachian tubes, tympanic cavity, and a part of the external auditory meatus and external ears which receive branches from the auricular branch of the vagus; and finally a portion of the back of the head which is supplied by the cervical spinal nerves. Some of the fibres of the trigeminus appear to belong to the nerves of taste (Chap. X.). Its *motor* fibres supply the muscles of mastication (temporal, masseter, mylo-hyoid and both pterygoids), the tensor tympani, tensor palati mollis, and probably also (Oehl) the dilatator iridis (Chap. X.). In addition, there run in the trigeminus vaso-motor fibres (probably of sympathetic origin) for the con-junctiva and iris. Finally, it contains *secreting* fibres for the lachrymal, parotid and submaxillary glands, concerning the origin and course of which, and their connection with the facialis, more is given on p. 96.

Some ascribe to the trigeminus fibres of a trophic character, destined

especially for the eyeball, since section of the trigeminus in the skull causes inflammation and degeneration of that organ. It is probable, however, that this result is to be attributed merely to loss of sensation which interferes with the protection of the eyeball from external influences; for no inflammation follows after section of the trigeminus, if a sensitive protective surface be artificially placed before the eyeball, *e.g.* in rabbits by stitching in front of it the ear which is supplied by the cervical nerves (Snellen). The latter explanation has recently been doubted. In the first place, after paralysis of the facialis, no inflammatory changes follow, notwithstanding that the animal thus paralysed is no longer able to protect its eye by closing the lid (Samuel). In the second place, after partial section of the trigeminal trunk in which the innermost fibres have been left intact, no inflammation is noticed, notwithstanding the complete sensory paralysis which occurs, and that the eye remains unprotected by artificial means; while, on the other hand, the eye becomes inflamed very easily (if not artificially protected), if in partial section the innermost fibres have been destroyed, notwithstanding that sensation still remains (Meissner, Schiff). If, therefore, the preceding isolated statements should be confirmed, and if the influence of vaso-motor fibres can be excluded, it will be necessary to resume the supposition of special 'trophic' fibres which course along the inner border of the trunk. The operation of these fibres is, as yet, quite unintelligible. The trigeminus is, moreover, said to contain trophic fibres for the cavity of the mouth, since section of that nerve occasions ulceration. The latter, however, depends upon the distortion of the lower jaw due to unilateral paralysis of masticatory muscles, whereby the teeth no longer meet, but press upon the mucous membrane opposite (Rollett).

Sixth pair (Abducens).—This is the motor nerve for the external rectus muscle of the eyeball (abducens).

The abducens receives, by anastomosis, fibres from the cervical portion of the sympathetic, so that the external rectus receives in addition fibres from the ciliospinal region of the spinal cord (Chap. XI.).

Seventh pair (Facial).—This nerve contains almost exclusively centrifugal (motor and secreting) fibres. Wherever it happens to possess sensory twigs it is due to the presence of fibres from the trigeminus, and, since section of the trigeminus does not cause complete loss of sensibility, to a slight extent from the vagus also. The chorda tympani, according to more recent theories, conveys gustatory fibres (Chap. X.).

Its *motor* fibres supply all the superficial muscles of the head,—the 'muscles of expression,'—the muscles of the external ear, the stylo-hyoid muscle, the levator palati, the posterior belly of the digastric muscle, the stapedius, and finally the platysma myoides. Its *secreting* fibres are connected with the salivary glands.

Paralysis of the facialis of one side causes contraction of the face towards the opposite side. This is due to the fact that, after contraction of the face, the tension of the paralysed muscles is not sufficient to stretch out the muscles of the opposite side to their previous length.

Eighth pair (Auditory nerve) (portio mollis of the seventh cranial nerve of Willis).—This is the only nerve connected with the perception of sound. Every irritation of it calls forth an auditory sensation, and section of it causes deafness. Concerning a noteworthy relationship between the auditory nerve and the position of the head, consult the Appendix to the Section on the sense of Hearing (Chap. X.).

Ninth pair (Glosso-pharyngeal) (part of the eighth cranial nerve of Willis).—This is a mixed nerve, which, however, only contains a few motor fibres for the following muscles: levator palati, azygos uvulæ, middle constrictor of the fauces, and stylo-pharyngeus. The remaining fibres are centripetal, and minister in part to the sense of touch, but chiefly to the sense of taste, of the soft palate and the root of the tongue.

Tenth and eleventh pairs (Vagus or Pneumogastric and Spinal Accessory of Willis).—Both together form a mixed nerve. It has been maintained (Longet) that these two nerves are to be regarded as two roots, of which one (Vagus) contains the centripetal, while the other (Accessorius), whose inner or anterior branch unites with the Vagus of descriptive anatomy, contains the centrifugal fibres. The vagus, however, at its origin, contains motor-fibres for the larynx, pharynx, and œsophagus (Van Kempen).

The centrifugal fibres, so far as is known, are the following:

a. Motor fibres. 1. For the muscles of the soft palate and the pharynx. 2. For the muscles of the larynx, contained for the most part, in the n. laryngeus inferior or recurrent laryngeal. The n. laryngeus superior supplies a branch for the crico-thyroid muscle: this statement has, however, been lately denied. 3. For the muscles of the bronchi: this is, however, doubtful. 4. For the œsophagus; after section of both vagi food which is swallowed no longer enters the stomach, while after section of the accessories no such result follows. 5. For the stomach (p. 101, 147). 6. According to some writers, for the small and large intestine and for the uterus. 7. For the sterno-cleido-mastoid and trapezius muscles, the fibres being situated in the outer or posterior branch of the accessorius of descriptive anatomy.

b. Regulating—inhibitory—fibres for the heart (Ed. Weber, Budge).

c. Secretory fibres. 1. For the glands of the gastric mucous membrane, &c.: this fact has not been conclusively proved, and has lately been contested.   2. For the kidneys (Bernard), since irritation of the vagus at the cardia is said to increase the urinary secretion, producing simultaneously arterialization of the venous blood (?).

d. Vaso-motor fibres for the vessels of the lungs (?).

The centripetal fibres are the following:

a. Sensory fibres supplying, in all probability: 1. The whole respiratory apparatus.   2. The digestive apparatus from velum palati to pylorus.   3. The heart.

b. Regulating fibres: 1. Accelerating for the inspiratory centre, arising probably in the lungs.   2. Inhibitory for the same centre (Rosenthal).   The distribution of these accelerating and inhibitory fibres among the branches of the vagus has been described on p. 167.   3. Stimulant for the cardiac inhibitory centres (Donders).   4. Stimulant for the vaso-motor centre ('pressor fibres'), especially in the superior laryngeal branch (Aubert and Roever).   5. Inhibitory for the same centre, which in many animals run in a special branch, the Ramus depressor nervi vagi (Ludwig and Cyon).   6. Stimulant for the salivary secretion, arising probably from the stomach (though this is doubtful: consult p. 94 *et sq.*).   7. Inhibitory for the pancreatic secretion (Ludwig and N. O. Bernstein).   8. Stimulant for the sugar-formation in the liver, *i.e.* fibres, the centripetal irritation of which calls into reflex activity the nerves which lead to the formation of sugar; these fibres have their peripheral terminations in the thorax, possibly in the lungs (Bernard).

The results of experimental section and irritation of the vagus and accessory, which have served to determine the various series of fibres contained in those nerves will now be gathered into a résumé.

1. Section of the spinal accessory above its point of union with the vagus (or, as is the usual plan, removal of the accessorius-roots from the cord), paralyses all the muscles dependent upon the vago-accessorius for their nerve-supply: according to some, the laryngeal muscles (van Kempen, Navratil) are not affected, and the power of swallowing is not entirely lost.   In addition section of the accessorius causes acceleration of the heart's action, while stimulation produces slowing (Waller, Heidenhain).   Unilateral paralysis of the external portion of the accessorius causes a twisting of the head.

2. Irritation of the vagus above the point of union with the accessorius

causes, among other things, contractions in larynx, pharynx, and œsophagus.

3. Section of the vagus-trunk in the neck causes (*a*) paralysis of laryngeal muscles and, in consequence, when both vagi are divided, inaction of the vocal cords, loss of voice and passage of portions of food into the lungs, whereby fatal pneumonia is induced; (*b*) quickening of the heart's action; (*c*) slowing of the movements of inspiration; (*d*) prevention of those reflex acts which stimulations applied to larynx, pharynx, and stomach, normally induce; (*e*) prevention of the last act in the operation of swallowing, so that the œsophagus becomes filled with food; (*f*) interruption of the sugar-formation in the liver (?).

4. Irritation of the peripheral portion of the divided vagus in the neck causes (*a*) spasms of the glottis or contraction of the laryngeal muscles, which is also induced by irritation of the peripheral end of the inferior laryngeal nerve; (*b*) slowing of the heart's action, and finally stand-still of that organ in diastole; (*c*) contraction (so it is said) of the smooth muscles of the bronchi, thus narrowing their lumen somewhat; this has, however, been frequently denied, by Donders, Wintrich, Rosenthal and Rügenberg, but has been again supported recently by Schiff; (*d*) contraction of stomach, intestine (?), uterus (?), &c.; (*e*) increased renal secretion (?).

5. Irritation of the central portion of the divided vagus in the neck causes (*a*) quickening of inspiratory movements which proceeds even to inspiratory tetanus; occasionally, however, an opposite result follows (p. 168); (*b*) increased sugar-formation (?); (*c*) increased salivary secretion (?); (*d*) diminished pancreatic secretion; (*e*) diminished blood-pressure if stimulation be applied above the point of union of depressor and vagus; (*f*) slowing of the heart's beat when the other vagus is intact.

6. Section or paralysis of the inferior laryngeal nerve paralyses the laryngeal muscles, causing the same phenomena as section of the vagus in the neck (see 3. *a*); aneurisms of the aortic arch sometimes press upon the left inferior laryngeal nerve, thus producing paralysis of the left vocal cord.

7. Section of the superior laryngeal nerve causes a slight slowing of inspiration (Sklarek), on account of the motor fibres for the larynx, and especially for the crico-thyroid muscle, which it contains. Nawratil has recently denied that the crico-thyroid muscle receives motor supply from this nerve.

8. Irritation of the central portion of the divided superior laryngeal nerve causes (*a*) slowing of inspiration which proceeds to complete cessation of the respiratory movements (Rosenthal); (*b*) increased blood-pressure by inducing contraction of the arteries.

9. Irritation of the central portion of the divided depressor branch of the vagus causes dilatation of all the arteries and, in consequence, a fall of blood-pressure (Cyon and Ludwig).

The irritability of the fibres of the vagus or, more correctly, of the end-organs of the fibres, varies with the fibre.

On irritation of the peripheral portion of a divided vagus, a stronger stimulus is needed to produce slowing of the heart than is necessary to produce contraction of the laryngeal muscles (Rutherford). During irritation of the central portion the fibres which cause quickening of respiration are

sooner exhausted than those which cause slowing (Burkart). The inhibitory fibres for the heart are sometimes very unequally divided between the two vagi (p. 74).

Twelfth pair (Hypoglossal).—This nerve is the motor nerve for all the muscles of the tongue, and, therefore, also the motor nerve concerned in speech. In addition it supplies the muscles connected with the os hyoides. It receives sensory fibres through its ramus descendens from the first cervical nerve, in consequence of which the tongue retains a certain amount of sensibility even after section of the trigeminus.

II. Spinal Nerves.

The centric course and origin of the spinal nerves is given in Chap. XI.

All the nerves springing from the spinal cord are, in a great part of their course, mixed. They are not so, however, at their origin, each arising by two roots,—an anterior, containing the centrifugal, and a posterior, containing the centripetal, fibres (Charles Bell). The former is called the *motor*, and the latter the *sensory*, root; the sensory root being provided with a ganglion.

If all the anterior roots of the nerves on one side be divided, the muscles on the corresponding side of the body become completely paralysed: while section of the posterior roots causes complete insensibility. If in an animal—a frog—we divide on the one side (say the right) the posterior, and on the other the anterior, roots of the lower spinal nerves, the following phenomena may be induced. If the *right* leg be irritated, no movements whatever occur, since the frog feels no pain; but if the left leg be irritated, movements for the purpose of avoiding the irritant take place in the *right* leg, since pain is felt in the left leg, while the right only is capable of motion. Moreover, in leaping, the frog drags its right leg just as it would a paralysed limb, because it no longer feels it.

The anterior roots are said sometimes to contain sensory fibres (Longet). They are, however, only such as proceed in reality from the posterior root and bend backwards into the anterior, after the roots have united to form the common trunk. Hence, after section of such anterior roots, it is only the peripheral portions which are sensitive, and sensibility is quite lost as soon as the posterior roots are also divided (Magendie).

The centrifugal fibres of the spinal nerves (contained in the anterior roots) are :

1. Motor fibres for all the transversely striated muscles of the trunk and extremities, and, probably through the medium

A A

of the sympathetic, for certain smooth muscles of the abdominal viscera also, as for example, for the muscular wall of the bladder. 2. Vaso-motor fibres for most of the arteries of the body ; they however, in part, first pass into the sympathetic system of nerves and then enter into other spinal roots (p. 76). 3. Possibly also secreting and trophic fibres. The centripetal fibres are the nerve-fibres of sensation for the whole surface of the body excepting the face and the forehead.

The distribution among the thirty-one pairs of spinal nerves of the various motor and sensory nerves destined for the different muscles and regions of surface falls under the province of anatomy.

If the posterior roots of the spinal nerves be divided, the irritability of the anterior roots suddenly sinks (Ludwig and Cyon ; the statement is, however, denied by Grünhagen and G. Heidehain). The former must, therefore, by a sort of reflex process, keep the irritability of the latter constantly increased, or, as is more intelligible, keep the latter under constant but weak stimulation (consult Chap. XI. on the tonus of muscle). If the last-mentioned supposition be correct, on irritation of the anterior roots, the stimulus applied will simply serve to increase that constant weak stimulation.

III. Sympathetic Nerves.

The consideration of the sympathetic nerves cannot well be separated from that of the sympathetic central organs, which will be found in Chap. XI., where, also, the reasons for such combined treatment are given at length.

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CHAPTER X.

THE PERIPHERAL END-ORGANS OF NERVES.

In discussing the organs engaged in secretion and motion the little which is known concerning the peripheral termination of *centrifugal* nerves has been referred to. The peripheral organs of *centripetal* nerves have in great part been accurately investigated. Many of these are in connection with contrivances which serve to transmit in a suitable manner to the end-organs the influences of the external medium, such as light, sound, heat, pressure, &c., which are capable of exciting nerves. For this purpose there exist organs which are composed both of conducting arrangements and end-organs of nerves, and which are called *Organs of the Senses.*

As the physiology of the conducting arrangements cannot be separated from that of the end-organs, the whole of the physiology of the Organs of the Senses will be here treated of.

I. THE ORGAN OF SIGHT.

In the organ of sight, the eye, the end-organs of the nerves terminate in a spherically curved membrane (the *retina*); the luminous impressions capable of exciting the sense of sight fall upon this surface. The rays of light which enter the eye are projected by means of a system of different refractive media upon the retina, in such a manner that a diminished, inverted and *real* image of the objects seen, is formed upon it, just as in a camera obscura.

Schema of the Eye.

The refractive media of the eye in the order in which they are traversed by the rays of light which fall upon them, are

the following : 1. The cornea. 2. The aqueous humor. 3. The lens with its capsule. 4. The vitreous body. Four separating surfaces (refracting surfaces) correspond to these media. 1. A surface between the air and the substance of the cornea (anterior surface of the cornea). 2. A surface between the cornea and the aqueous humor (posterior surface of the cornea) &c. In order to be able to follow the paths of luminous rays which pass through the eye to the retina, the following data must be known : 1. The refractive indices of all the media. 2. The forms of all the refracting surfaces. 3. The distances of these from one another and from the surface upon which the image is projected (retina).

The crystalline lens is not a simple refracting medium ; its consistence and its power of refraction increase from the exterior to the interior, its solid nucleus, which is of very small radius of curvature, refracting light most powerfully.

The annexed diagram, Fig. 12, which represents in a simplified manner the structure of the lens, shows that it may be looked upon as made up of a powerful convex lens c and of two concave lenses a and b. The latter neutralize to a certain extent the action of c, and they do so the less the smaller their refractive index. In as much as a and b possess a smaller index of refraction than c, the action of the lens as a whole is greater than it would be if they had the same index of refraction as c, i.e. it is greater than would be the case were the lens composed of homogeneous matter having the same index of refraction as the nucleus. The focal distance of the lens being determined by experiment, and its shape being known, the so-called total index of refraction of the lens may be calculated, i.e. the index of refraction which the lens would possess, were it homogeneous. According to what was said previously it follows that the index thus calculated is greater than that of the nucleus.
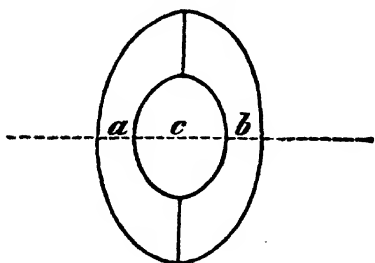
The optical problems connected with the eye are much simplified by the fact that the cornea is a membrane the surfaces of which are parallel, and which limits anteriorly and posteriorly fluids which possess approximately the same index of

refraction (in front is the lachrymal fluid which moistens it, behind the aqueous humor); such a body (like a plate of glass the surfaces of which are in contact with air, *e.g.* a window-pane or a watch-glass) cannot give a new direction to a ray of light which traverses it, but can only deviate it slightly in a direction parallel to itself. The cornea itself may therefore be entirely neglected, and we may reason as if the aqueous humour extended to the anterior surface of the cornea. There remain, therefore, only three refracting media to be taken into account, the *aqueous humour*, the *lens*, and the *vitreous body*, in addition to three refracting surfaces, viz. the *anterior surface of the cornea* and the *anterior* and *posterior surfaces of the crystalline lens.* The centres of curvature of these three surfaces lie in one straight line—the *optic axis.*[1]

The following data apply to the eye when at rest (i.e. when not *accommodated* for distance) (Listing).

(*a.*) The refracting surfaces are spherical surfaces the radii of which have the following measurements:

1. The anterior surface of the cornea about 8^{mm}
2. The anterior surface of the lens   „ 10^{mm}
3. The posterior surfaces of the lens   „   6^{mm}

(*b.*) The distances between these refracting surfaces are—

from 1 to 2   .   .   .   .   about 4^{mm}
„   2 to 3 ('axis of the lens')   „   4^{mm}
„   3 to the retina   .   .   .   „   13^{mm}

(*c.*) The *indices* of *refraction* are (that of air being taken as 1) for the aqueous humour $\dfrac{103}{77}$

for the lens (*total*) $= \dfrac{16}{11}$

for the vitreous body $= \dfrac{103}{77}.$

The results of the most accurate of these determinations (Brewster, the two Krauses, Helmholtz) cannot here find a place; only the methods which have been employed in making them can be shortly indicated. The refractive indices of the fluid media have been determined in the media of eyes removed from the body by well-known optical methods; the total refractive

[1] When examined under water the action of the anterior surface of the cornea also ceases, so that the eye under these circumstances possesses but two refracting surfaces. The consequences of this will be seen further on.

index of the lens is calculated from its empirically determined focal distance and from its external form. The determination of the radii of curvature must when possible be determined in the living eye, as the forms undergo various changes (see below). This determination is made by the following very exact method, which is specially of importance in ascertaining exactly the changes which occur during accommodation (Helmholtz). According to simple geometrical principles the radius of a spherical surface may be calculated by placing a body of linear form and of known length at a measured distance from it, and measuring the image of the body reflected at the spherical surface. These measurements are effected in the following manner: the corneal image, which we shall suppose to be horizontal, is observed through a thick glass plate. This plate is divided horizontally into two halves, which are movable around a common vertical axis. So long as the rays of light pass perpendicularly through the glass plate, the reflected image appears unchanged; if now the two glass plates are turned around their axis, but from opposite sides (so that looked at from above they appear crossed), each plate is struck obliquely by the rays, and in con-sequence the image is displaced in a horizontal direction. The two plates displace the image in opposite directions, and there appear *two* images; if now the plates have been turned to such an extent that the image seen through each is displaced through a distance of one half of its length and that the opposite terminal points of the two images touch (one image appearing to be a prolongation of the other), the length of the image may be calculated from the angle which the two plates make one with the other, providing that the thickness and refractive index of the plates be known. Such an apparatus, so arranged that the angle between the plates may be read off, is termed an 'Ophthalmometer.' In reference to the distance between the refracting surfaces, it may be said that the thickness of the lens (*i.e.* the length of the axis of the lens) may be determined in lenses removed from the eye. Yet it is better, on account of the changes which it undergoes physiologically, to effect this measurement by means of the Ophthalmometer, in the living eye, from the reflected images; the same method is followed in determining the distance between the anterior surface of the cornea and the anterior surface of the crystalline lens.

Formation of the Image.

According to the statements which have been made, the eye is a system composed of three *concentric* refracting surfaces. The laws of refraction of such a system may be explained as follows.

1. Let c d (Fig. 13) be a spherically curved refracting surface, k the centre of curvature, and a b a straight line which passes through it, *the axis.* Let c d separate two media, of which the one to the left (the *anterior* or first) possesses the refractive index *m*, the other (the *posterior* or second) the index *n.*

The luminous ray e g falling from the point b on the axis in the first

medium upon the surface C D is refracted at G; the perpendicular to the tangent-plane at the point G is the radius K I, therefore E G I = p is the angle of incidence, K G L = q is the angle of refraction. According to the law of refraction F G, K I and G L lie in one plane, so that G L must like E G cut the axis. Let the distance, E H, of the point E from the *principal point*
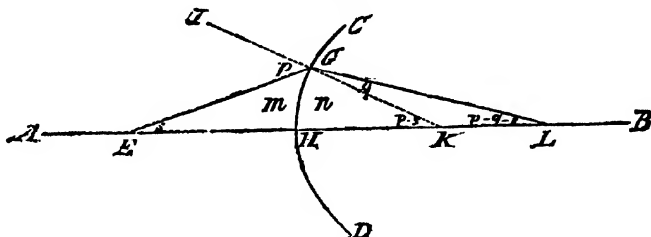
H, be equal to a_1, and the distance of the point L from the principal point H, L H, be equal to a_2. The relation of the distances a_1 and a_2 is then obtained in the following manner (let the angle H E G = s, then the angle H K G = $p - s$, and the angle H L G = $p - q - s$; lastly, let the radius K H = K G = r).

According to the law of refraction

$$\sin p : \sin q = n : m \ldots \ldots \ldots (1)$$

In the triangle E G K

$$a_1 + r : r = \sin (180° - p) : \sin s \ldots \ldots (2)$$

And in the triangle G K L

$$a_2 - r : r = \sin q : \sin (p - q - s) \ldots \ldots (3)$$

If E and H are very distant from one another, or if G and H are very close to one another, then the ray E G is only slightly bent from the direction of the axis, and if it falls upon the refracting surface near the axis, the angles p, q, and s are so small that one may consider their sines to the arc as equal. If one does this, and if one considers that $\sin (180° - p) = \sin p$, then

$$(1) \text{ becomes } n q = m p \ldots \ldots \ldots \ldots (4)$$
$$(2) \ldots \ldots p r = s (a_1 + r) \ldots \ldots \ldots (5)$$
$$(3) \ldots \ldots q r = (p - q - s)(a_2 - r) \ldots (6)$$

If in these three equations we eliminate q and s, p vanishes, and we obtain the following simple relation between a_1 and a_2:

$$\frac{m}{a_1} + \frac{n}{a_2} = \frac{n - m}{r} \quad (7)$$

As this relation is independent of the angles p and s, all other rays falling from E upon C D (always assuming that the angles p and s are not too large) must, after being refracted, pass through the point L. A 'homocentric' pencil of rays proceeding from E must, therefore, after refraction again be homocentric; the point of intersection after refraction is termed *the image* of the luminous spot E.

2. If the point E be not situated in the axis, a straight line may always be drawn through it and the nodal point K, and this line may be looked upon as a new axis; the image L then lies in this line.

3. The law of homocentric pencils of light applies wherever the point E may be situated. A point of intersection of the rays proceeding from it corresponds to every luminous point, and this point of intersection always lies in a straight line, joining the luminous point and the nodal point; this line is called the *principal ray* or *line of direction*.

The image is called *real* when the rays, as in Fig. 14, pursuing their proper direction, form it; it is called *virtual* when it is not formed by the rays, but is only obtained by prolonging them backwards.

4. If the positions are reversed and the refracted rays be regarded as the incident rays (the *real* or the *virtual* point in the image becoming the real or virtual point of exit of rays), these will again unite, as the most superficial consideration teaches us, at the original luminous points.

The luminous point and the image have, therefore, a reciprocal relationship, and they are, for this reason, more correctly designated ' conjugate foci,' and their respective distances from the principal point (a_1 and a_2 in §1), as ' conjugate focal distances.'

5. If in Fig. 13 the incident ray E G be parallel to the axis, then $E H = a_1 = \infty$, and in equation (7) $\frac{m}{a_1} = 0$, and consequently a_2 acquires the value

$$\frac{n\,r}{n-m} = f_2 \ . \ . \ . \ . \ . \ . \ (8)$$

Fig. 14.
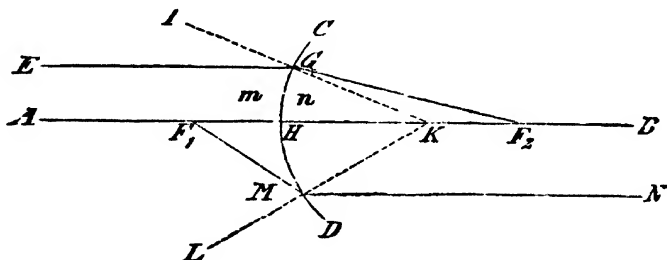
Conversely, if the ray L G coming from the second medium be parallel to the axis, then

$$L H = a_2 = \infty, \text{ and in equation (7), } a_1 \text{ acquires the value}$$

$$\frac{m\,r}{n-m} = f_1 \ . \ . \ . \ . \ . \ . \ (9)$$

Thus all rays which are in the first instance parallel to the axis unite after refraction at a point F_2 (Fig. 14) which may be termed the *posterior or second focal point*, and the distance of which from the principal point $H\,F_2 = f_2$ (equation 8) is termed the *second focal distance*. Similarly all those rays which are parallel to the axis in the second medium, unite to form the *first or anterior focal point* F_1, the distance of which from the centre of curvature, $H\,F_1 = f_1$ (equation 9), is termed the *first focal distance*. (Con-

versely all rays which proceed from the focal points, become parallel after refraction.)

6. From (8) and (9) it follows further that

$$f_1 : f_2 = m : n \quad \ldots \ldots \quad (10)$$
$$f_2 - f_1 = r \quad \ldots \ldots \quad (11)$$

i.e. the first and the second focal distances are related to one another as the indices of refraction of the first and second media, and the difference between these focal distances is equal to the *radius of curvature*; thus in Fig. 15, H F$_1$ = K F$_2$, *i.e.* the distance of the first or anterior focal point from the principal point H is equal to the distance of the second focal point from the nodal point.

7. The focal points can very usefully be employed in order to find geometrically the image s$_2$, which corresponds to a luminous point s$_1$.

In Fig. 15, let H again be the principal point, K the nodal point, F$_1$ and F$_2$ the two focal points. The point of intersection of any two refracted

FIG. 15.
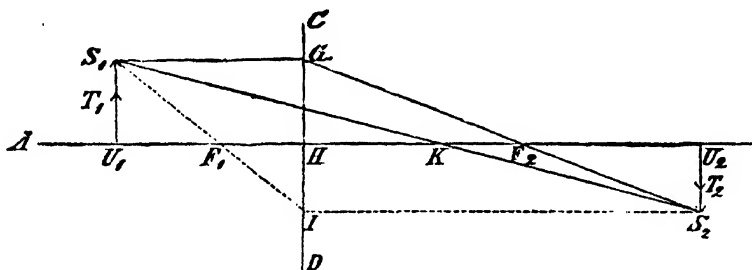
rays proceeding from s$_1$ must be the point of intersection of all other rays. In order to find this point of intersection we may best make use of the following rays : 1. The unrefracted principal ray, s$_1$ K s$_2$; 2. the ray, s$_1$ G, which pursues a course parallel to the axis and passes after refraction through the second focal point, viz., which pursues the course G F$_2$ s$_2$; 3. The ray s$_1$ F$_1$ I, which passes through the first (or anterior) focal point, and which after refraction is parallel to the axis, pursuing the line I s$_2$. Any two of these rays suffice in order to find s$_2$, and it is easy to prove geometrically that they all pass through s$_2$.

By the same construction we can further find that any luminous point T, situated in the line s$_1$ U$_1$ perpendicular to the axis, will throw its image on the perpendicular s$_2$ U$_2$, at the point T$_2$. All points lying in a plane perpendicular to the axis therefore form images on a plane which is also perpendicular to the axis. Every flat object which is perpendicular to the axis furnishes therefore a flat image perpendicular to the axis, which really, as can readily be proved by geometrical methods, resembles the object.

From § 6 it follows that all luminous points situated at an infinite distance (from the refracting surface) throw their image on a plane which is perpendicular to the axis at the focal point ; this plane is termed the *focal plane*. Rays which are parallel to one another, therefore, always intersect at one point of the focal plane.

8. From the preceding there results a simple method of constructing the course of the refracted ray G I, which corresponds to the incident ray E G (Fig. 16). Let O P be the focal plane. A ray parallel to E G must intersect the required (refracted) ray at some point (M), situated in the focal plane.

FIG. 16.
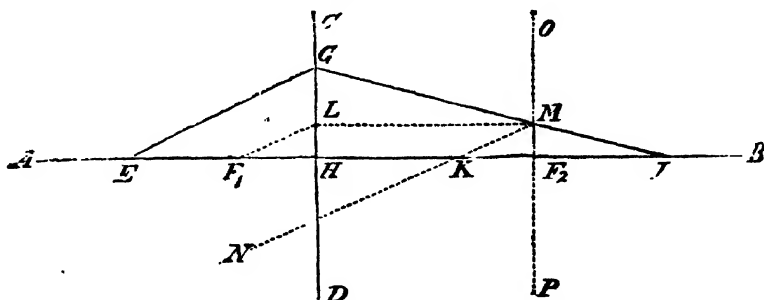
In order to find this point we may either make use of the unrefracted principal ray N K M which is parallel to E G, or we may draw through the focal point F₁ a parallel ray (F₁ L), parallel to E G, which will after refraction pursue a course parallel to the axis and will so lead to M.

9. If in Fig. 15 (§ 7) we take H U₁ = a_1 and H U₂ = a_2, further if the size of the object U₁ S₁ = l_1, the size of its image U₂ S₂ = $-l_2$ (it has a negative sign as it lies below the axis) the following relations are found:

In the similar triangles S₁ U₁ F₁ and I H F₁

$$a_1 - f_1 : l_1 = f_1 : -l_2 \ \ldots \ldots \ (12)$$

In the similar triangles S₂ U₂ F₂ and G H F₂

$$a_2 - f_2 : -l_2 = f_2 : l_1 \quad (13)$$

From (12) it follows $\dfrac{l_1}{l_2} = 1 - \dfrac{a_1}{f_1} \ \ldots \ (14)$

From (13) $\qquad\qquad \dfrac{l_2}{l_1} = 1 - \dfrac{a_2}{f_2} \ \ldots \ (15)$

Lastly from (15) and (16) $a_1 f_2 + a_2 f_1 = a_1 a_2$ or $\dfrac{f_1}{a_1} + \dfrac{f_2}{a_2} = 1 \ \ldots \ (16)$

The equation (16) passes into equation (7) if we substitute for f_1 and f_2 the values furnished by equations (8) and (9).

10. If in equation (16), we give to a_1 all values between ∞ and 0, a_2 acquires the following values:

(1) when $a_1 = \infty$ (the luminous point being infinitely distant) $a_2 = f_2$
(image situated at F₂, see § 5)

(2) „ $a_1 = f_1$ (luminous point at F₁) $a_2 = \infty$ (image infinitely distant, see § 5)

(3) „ $a_1 = 0$ (luminous point at H) $a_2 = 0$ (image coincides with H)

(4) „ $a_1 = -(f_2 - f_1)$ [1] (luminous point at K) $a_2 = f_2 - f_1$ (image coincides with K).

[1] a_1 must always be reckoned as positive when it is on the left of H, negative when it is on the right; a_2, on the contrary, is reckoned positive when it is on the right side.

The principal point and the nodal point coincide with their own images.

11. Planes which intersect conjugate foci at right angles to the axis may be called *conjugate planes*, for the images of objects on the one plane are thrown upon the other. The relation between the size of these images is expressed by l_1 and l_2 (compare § 9). Every point in one plane has therefore an image which corresponds to it in the other, and the distances of these points from the axis are as $l_1 : l_2$. If, therefore, one knows the situation and relation between the sizes of the images on two conjugate planes, we may make use of any point for constructing the image; for every ray which passes from this point in the anterior plane must after refraction pass through a perfectly definite point of the posterior plane. If now in the construction we select two rays which obey also the condition of passing through the foci, they are *ipso facto* perfectly determined. It is naturally most convenient for the purpose of these constructions to select those conjugate planes, the images in which are not merely similar, but of equal magnitude, and which are called *principal planes*.

Their situation is found when in equations (15) and (16) $l_1 = l_2$. It follows then that $a_1 = 0$ and $a_2 = 0$, i.e. the two *principal planes* coincide not only with one another but also with the refracting surface.

12. In the case of two spherically curved refracting surfaces, a straight line which joins their *centres of curvature* constitutes their common axis. As a homocentric pencil of rays falling upon the first surface (providing that its rays do not form too great an angle with the axis) continues homocentric even after refraction, and therefore falls homocentrically upon the second surface, it follows that even after issuing from the second surface the rays are homocentric.

13. Let the distance of the two refracting surfaces along the axis be e; further let f_1, f_2 be the focal distances of the first and g_1, g_2 those of the second surface. Let now a_1 be the distance of an object from the first surface, then the first surface casts an image at distance a_2 behind itself.

If this image be situated at the distance b_1 in front of the second refracting surface, then the image cast by this is situated at a distance b_2 behind. The following relations are found to exist:

from (16)
$$\frac{f_1}{a_1} + \frac{f_2}{a_2} = 1$$

from (16)
$$\frac{g_1}{b_1} + \frac{g_2}{b_2} = 1$$

lastly
$$a_2 + b_1 = e$$

Hence
$$b_2 = \frac{(a_1 e - f_1 e - f_2 a_1)\, g_2}{(e - f_2 - g_1)\, a_1 - (e - g_1)\, f_1}. \quad \ldots \ldots \quad (17)$$

14. Further, if l be the size of the object, l_2 that of its image after passing through the first refracting surface, m_2 the ultimate image after refraction by the second surface, it follows from

(14) that
$$l_2 = \frac{f_1}{f_1 - a_1} \cdot l_1$$

from (15) that
$$m_2 = \frac{g_2 - b_2}{g_2} \cdot l_2$$

If for b_2 we substitute the value found by (17) we obtain :

$$m_2 = \frac{f_1 g_1 l_1}{(e - f_2 - g_1) a_1 - (e - g_1) f_1} \quad \cdots \cdots \quad (18)$$

15. If it be required to find the positions of the *principal planes* (§ 11), we must in (18) make $m_2 = l_1$; the distance of the first principal plane from the first refracting surface is then found by the following equation :

$$a_1 = - \frac{f_1 e}{e - f_2 - g_1} \quad \cdots \cdots \cdots \quad (19)$$

The distance of the second principal plane from the second refracting surface is found by substituting the value found by equation (19) for a_1 in equation (17):

$$b_2 = \frac{g_2 e}{e - f_2 - g_1} \quad \cdots \cdots \cdots \quad (20)$$

The two principal planes do not therefore coincide, but are separated from one another by

$$a_1 + b_2 + e.$$

16. The ultimate focal point of the rays which before passing through the first refracting surface were parallel to the axis (i.e. the *principal focal point* or *focus*) is formed by making $a_1 = \infty$ in equation (17) ; b_2 is then the distance of the posterior principal focus from the second refracting surface, and

$$B_2 = \frac{(e - f_2) g_2}{e - f_2 - g_1} \quad \cdots \cdots \cdots \quad (21)$$

Conversely the *anterior principal focal point*, corresponding to the rays, which after the last refraction become parallel to the axis, is found by equation (17), making $b_2 = \infty$; a_1 is then the distance of the anterior focal point from the first refracting surface, and

$$A_1 = \frac{(e - g_1) f_1}{e - f_2 - g_1} \quad \cdots \cdots \cdots \quad (22)$$

17. The distance of the first (anterior) principal focus from the first principal point, *i.e.* the *first anterior* focal distance is $A_1 - a_1 = F_1$, therefore

$$F_1 = \frac{f_1 g_1}{f_2 + g_1 - e} \quad \cdots \cdots \cdots \quad (23)$$

Corresponding to this is the distance of the second (posterior) focal point from the second principal point, *i.e.* the second chief focal distance $B_2 - b_2 = F_2$, therefore

$$F_2 = \frac{f_2 g_2}{f_2 + g_1 - e} \quad \cdots \cdots \cdots \quad (24)$$

From (23) and (24) we obtain

$$F_1 : F_2 = f_1 g_1 : f_2 g_2 \quad \cdots \cdots \cdots \quad (25)$$

If now m be the refractive index of the first, n that of the second, o that of the third medium, it results (from 10, § 6)

$$f_1 : f_2 = m : n$$
$$\underline{g_1 : g_2 = n : o,}$$
$$f_1 g_1 : f_2 g_2 = m : o, \quad \text{therefore}$$
$$F_1 : F_2 = m : o \quad \cdots \cdots \cdots \quad (26)$$

i.e. *the two principal focal distances bear the same relation to each other as the indices of refraction of the first and last medium.*

18. With the help of the two principal planes ($h_1 h_1$ and $h_2 h_2$ in Fig. 17), and of the two principal focal points F_1 and F_2, we can easily construct the image s_2, which corresponds to any given luminous object s_1; here again two rays are made use of. The ray $s_1 c_1$ proceeding from the point s_1 in a direction parallel to the axis, passes after refraction through c_2, and F_2,

FIG. 17.
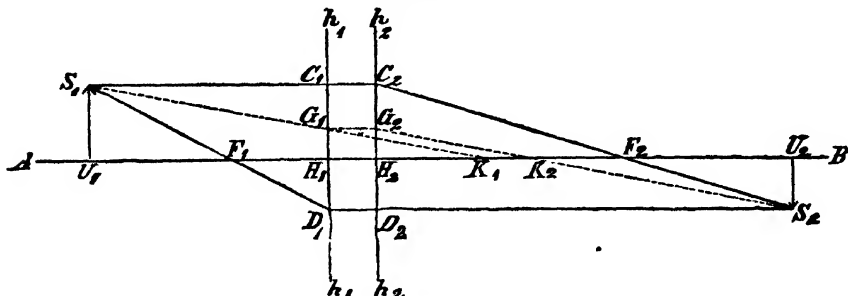
and must therefore follow the path $c_2 F_2 s_2$. The ray $s_1 D_1$ which passes from s_1 through F_1 must, after refraction, at first be parallel to the axis, then pass through the point D_1 on the second refracting plane which corresponds to the point D_1 on the first, and therefore it must pursue the path $D_2 s_2$, and s_2 must therefore be the image sought for, which corresponds to s_1.

19. If now the lengths $H_1 U_1 = A_1$ and $H_2 U_2 = A_2$, *i.e.* if the conjugate focal distances be calculated from the principal points, we obtain from an examination of the similar triangles in *Fig.* 17, eq. (16), corresponding to an equation

$$A_1 F_2 + A_2 F_1 = A_1 A_2 \quad \cdots \cdots \cdots \quad (27)$$

If in this equation $A_2 = -A_1$, we obtain

$$A_1 = F_2 - F_1 \quad \cdots \cdots \cdots \cdots \quad (28)$$

which is the distance of that point from the first principal plane, the image of which lies just as far behind the second principal plane.

We have now two new conjugate foci, the two *nodal points* (K_1 and K_2 in Fig. 17), which are distant from one another to the extent of the difference of both principal focal distances from the principal points. (In the case of a simple refractive surface, there is but a single nodal point, § 2). As the two nodal points are conjugate points, each ray, which after the first refraction is directed towards K_1, *e.g.* $s_1 K_1$, *i.e.* each so-called *principal ray*, must after the second refraction pass through K_2, and must be parallel to $s_2 K_1$, therefore fall on $G_2 s_2$, because it has yet to satisfy the other condition, *i.e.* to cut the second principal plane at the point G_2, which corresponds to G_1 (see § 18). It may be easily seen that, in the construction of the image of s_1, instead of one of the two rays $s_1 c_1$ or $s_1 D_1$, the ray $s_1 K_1$ might also be employed. (The two nodal points are hence axial points possessed of the following characters; each ray which before refraction is directed to the first point, passes after refraction through the second, in a direction parallel

to that of incidence.   From this property, the position of the nodal points
may be directly determined.)

20. If to the previously considered system, composed of two refracting
surfaces, we add yet a third refracting surface, or a second system composed
of two refracting surfaces, the same simplification may as before be admitted,
as long as all the refracting surfaces have a common axis (are concentric), *i.e.* as
long as their centres of curvature lie in the same straight line (which could
naturally only be constantly the case with two surfaces); for only under these
circumstances will a homocentric bundle of rays, falling upon each succeed-
ing surface, make so small an angle with the axis as to continue homo-
centric.   It is always possible then to give, in the case of the whole system,
the situation of the *cardinal points*, which serve in the construction of the
image, and which are, viz., the two *principal points*, the two *focal points*, and
the two *nodal points*.

If the focal distances of two systems have been found, and the distance
of their principal planes known, the cardinal points of the resulting system
can always be found by means of equations 19-24 and 28.

In order to find the cardinal points for the compound system
of the eye, the focal distances of each single refracting surface
must be ascertained.   Equations (8) and (9) or (8) and (11)
are employed with this object.

1. Anterior surface of the cornea: $r = 8^{mm}$, $m = 1$, $n = \dfrac{103}{17}$.

   Therefore $f_1 = 23\cdot692^{mm}$, $f_2 = 31\cdot692$.

2. Anterior surface of the lens: $r = 10$, $m = \dfrac{103}{77}$, $n = \dfrac{16}{11}$.

   Therefore $f_1 = 114\cdot444$, $f_2 = 124\cdot444$.

3. Posterior surface of the lens: $r = -6$, $m = \dfrac{16}{11}$, $n = \dfrac{103}{77}$.

   Therefore $f_1 = 74\cdot667$, $f_2 = 68\cdot667$.

If 2 and 3 be now combined so as to form one (optical) system,
i.e. if the cardinal points of the lens surrounded by the fluids
of the eye be wanted, $e = 4^{mm}$, $f_1 = 114\cdot44$, $f_2 = 124\cdot44$, g_1
$= 74\cdot667$, $g_2 = 68\cdot667$.   Therefore:

   the first principal point of the lens is situated behind the
      anterior surface of the lens (according to 19) by
      about $- a_1 = 2\cdot346^{mm}$;

the second principal point of the lens is situated in front of the posterior surface of the lens (according to 20) about $- b_2 = 1.408^{mm}$;

the two focal distances of the lens, which according to 26, in consequence of the indices of refraction of the aqueous and vitreous humour being equal, are equal, are (according to 23 or 24) $F_1 = F_2 = 43.797^{mm}$.

If now, finally, the cornea is combined with the lens as in the complete system of the eye, we have in this combination:

$$f_1 = 23.692, f_2 = 31.692, g_1 = 43.797,$$
$$g_2 = 43.797, e = 4 + 2.346 = 6.346^{mm}.$$

In the case of the eye as a whole

the first principal point is situated (according to 19) at $-a_1 = 2.174^{mm}$ behind the convexity of the cornea;

the second principal point is situated (according to 20) at $-b_2 = 4.020^{mm}$ in front of the second principal point of the lens, therefore $4.020 + 1.408 = 5.428^{mm}$ in front of the posterior surface of the lens, or 2.572^{mm} behind the convexity of the cornea;

the two principal points are therefore distant from one another by 0.398^{mm}.

The first principal focal distance is (by 23) $F_1 = 15.007^{mm}$, the first focal point is situated therefore 12.833^{mm}, in front of the convexity of the cornea;

the second principal focal distance is (by 24) $F_2 = 20.074^{mm}$, the second focal point is situated therefore 22.646^{mm} behind the convexity of the cornea.

As the distance of the nodal points from the principal points $= F_2 - F_1 = 5.067$

the first nodal point is situated 7.241^{mm} behind the convexity of the cornea, and

the second nodal point is situated 7.639^{mm} behind the convexity of the cornea.

The two principal points are therefore 0.398^{mm} from one another, about the middle of the anterior chamber of the eye; the two nodal points lie similarly 0.398^{mm} from one another, in the posterior part of the lens, the second focal point being either close to or in the retina.

Figure 18 exhibits the schematic eye with its cardinal points.

The distance between the two nodal points is so small that in drawings intended for purposes of demonstration they may, without introducing any great error, be united at κ ; similarly the principal rays may be simply represented by straight lines. (Likewise the two principal planes may be imagined united in the spherical surface *hh,* which therefore represents the refracting surface of the eye.)   If we suppose that all points in the image lie on the retina (on this subject refer to what is said on *Accommodation*), we can for every point in the object easily find the corresponding point in the image, by drawing from the former a straight line passing through the nodal point and falling upon the retina.

Such straight lines (*e.g.* o b in Fig 18) are called *lines of direction* or visual rays, and the combined nodal points (κ) are

Fig. 18.
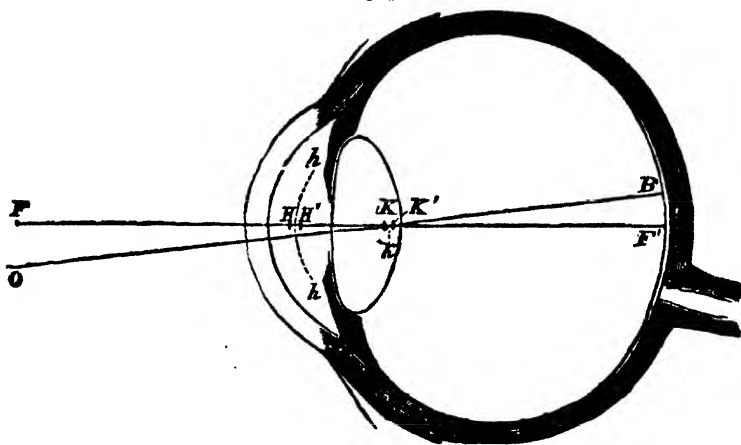
included under the terms *point of intersection of lines of direction* ; the angle which two visual rays make with one another, is called the *visual angle.* If it be desired to ascertain the direction in which lies the point of an object which corresponds to any point in an image, it is only necessary to draw a straight line (*a visual ray*) from the point on the image through the combined nodal points, and to prolong it outwards.

Appendix on the Action of Lenses.

In the case of a lens, which is bounded on both sides by atmospheric air, the two principal focal distances are (according to equation 26) equal; by (28), in consequence of this, the nodal points coincide with the principal points.

In order to find the value of the focal distance, let the two radii of cur-

vature of a biconvex lens be r_1 and r_2, let n be the index of refraction (the index of refraction of the atmosphere being 1); then the four focal distances of the two surfaces are by 8 and 9 :

$$f_1 = \frac{r_1}{n-1}, \quad f_2 = \frac{nr_1}{n-1}, \quad g_1 = -\frac{nr_2}{1-n}, \quad g_2 = -\frac{r_2}{1-n}$$

It follows from (23) or (24), that if the thickness of the lens, e, be neglected

$$\frac{1}{F} = (n-1)\left(\frac{1}{r_1} + \frac{1}{r_2}\right) \quad \dots \quad \dots \quad (29)$$

If one of the surfaces be concave, its radius must be considered to be negative. Biconcave and concavo-convex lenses (in which the concave surface has the smaller radius) have, therefore, negative focal distances.

If two lenses, having the focal distances f and g, be placed so close one behind the other that the distance between them, e, may be neglected, it follows from (23), F being the focal distance of the combination, that

$$F = \frac{fg}{f+g} \quad \text{or} \quad \frac{1}{F} = \frac{1}{f} + \frac{1}{g} \quad \dots \quad \dots \quad (30)$$

Similarly for a combination of several lenses in proximity,

$$\frac{1}{F} = \Sigma\left(\frac{1}{f}\right) \quad \dots \quad \dots \quad \dots \quad (31)$$

Let a_1 be the distance of an object from a lens, l_1 its size, f the focal distance, and a_2 and l_2 the distance and size of the image, it follows from (16),

$$\frac{1}{a_1} + \frac{1}{a_2} = \frac{1}{f} \quad \dots \quad \dots \quad \dots \quad (32)$$

further from (14),

$$\frac{l_1}{l_2} = 1 - \frac{a_1}{f} \quad \dots \quad \dots \quad \dots \quad (33)$$

From the above the characters of the image formed by each kind of lens may be ascertained ; the most important are given below. a_1 and l_1 are always assumed to be positive.

I. Convex lenses (f being positive).

    1. a_2 is positive, *i.e.* the images are real, when $a_1 > f$;
        a_2 is negative, *i.e.* the images are virtual, when $a_1 < f$.
    2. l_2 is negative, *i.e.* the images are inverted, when $a_1 > f$;
        l_2 is positive, *i.e.* the images are erect, when $a_1 < f$.
    3. $l_2 < l_1$, *i.e.* the images are diminished, when $a_1 > 2f$;
        $l_2 = -l_1$, when $a_1 = 2f$;
        $l_2 > l_1$, *i.e.* the images are enlarged, when $a_1 < 2f$.

Hence a convex lens gives, when $a_1 > 2f$, real, inverted, diminished images (object-glasses of telescopes, opera-glasses, and cameræ obscuræ); when $2f > a_1 > f$, the images are real, inverted, and magnified (solar microscope, object-glass of the compound microscope); lastly, when $a_1 < f$, the images are virtual, erect, and magnified (simple magnifying glass, eye-piece of astronomical telescopes and of compound microscope).

II. Concave lenses (f negative).

    1. a_2 is always negative,

2. l_2 is always positive,

3. l_2 is always $< l_1$.

Concave lenses always furnish virtual, erect, and diminished images of objects.

If a convex lens be so placed that it furnishes a real, inverted image of an object, and if a second lens be placed in the path of the refracted rays, before they have united to form the image, the rays form the object for the second lens ; the distance of the former from the latter, a_1, is, however, to be considered as negative.

The action of the lens thus interposed is as follows :—

I. When the interposed lenses are convex (f is positive). For every negative value of a_1, a_2 becomes positive, $a_2 < -a_1$, l_2 has the same sign as, but is less than l_1, *i.e.* the interposed convex lens furnishes a real inverted image, but brings it closer to the first lens and diminishes its size. The collecting lens of the compound microscope exerts this action.

II. When the interposed lenses are concave (f is negative).

1. a_2 is positive when $-a_1 < f$, and negative when $-a_1 > f$.

2. l_2 has the opposite sign to l_1 when $-a_1 < f$, and the same sign when $-a_1 > f$.

3. $l_2 < l_1$ when $-a_1 > 2f$; $l_2 = l_1$ when $-a_1 = 2f$; $l_2 > l_1$, when $-a_1 < 2f$.

When a concave lens is interposed between a convex lens and a *real* image, the latter continues to be *real* and *inverted*, providing that the lens is situated at a distance from the image less than its focal distance ; on the contrary, the image becomes virtual and erect if the concave lens is more than its focal distance from the image formed by the first lens ; the eye-piece lens of opera-glasses has this property. It does not alter the size of the image, if it be at a distance from the object equal to twice its focal length.

On the Images formed on the Retina when the Eye is passive.

When luminous rays proceeding from any object fall into the eye, a definite point in the image corresponds to every point in the object. All the points of the image together furnish an image which corresponds to the object; the image is, naturally, an inverted one. In order to be distinctly perceived, this image must fall exactly upon the surface of the retina. It is evident that for any given eye remaining perfectly passive, there can be only a single surface, the image of which can fall exactly on the retina. The form and the distance of this surface may be determined from the optical values of the eye. Each point of the object which does not ·lie in this surface has its corresponding point in the image lying, not in the retina, but in a plane before or behind it. In both cases the retina cuts the pencil of refracted rays proceeding from the object ; in the first case after, in the second before, they have united to form

points in the image'; in both cases, instead. of a luminous point being formed on the retina, there ' is a circle of diffused light,' *i.e.* a small circular area is lighted up; this corresponds to a section through the luminous cone.

In Fig 19, B represents the point of the image of the object O, which falls upon the retina *r r*. If, however, the retina lies

FIG. 19.
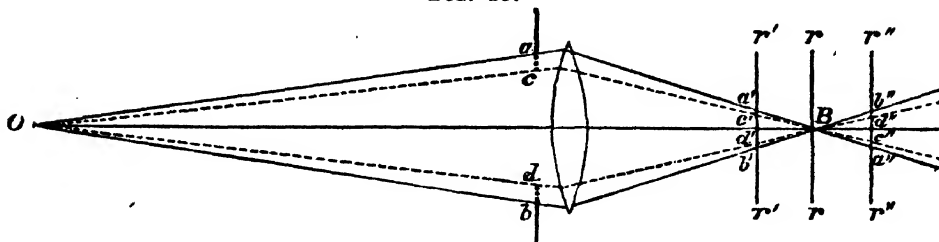
in front of the point in the image (*viz.* at *r′ r′*), or behind it (*e.g.* at *r″ r″*), circles of diffused light are formed, which have the diameters *a′ b′* or *a″ b″*.

Hence it follows that, strictly, an immovable eye can only distinctly see objects lying in one plane, and at a perfectly definite distance.   All objects or portions of objects which lie outside the plane, furnish indistinct, blurred, images, in which *circles of diffusion* instead of points correspond to the luminous points of the object.

The size of the circle of diffusion depends, *cæteris paribus*, upon the dimension of the cone of luminous rays which reaches the eye, and this again depends upon the width of the pupil, the inner border of which limits the luminous cone.   If therefore the pupil contracts, or if it be replaced by a small aperture placed in front of the eye, as *e.g.* by a hole made in a card, then the circles of diffused light will, *cæteribus paribus*, become smaller, and consequently the image will be sharper.   In Fig. 19, if *c d* represents the aperture of the contracted pupil, it can be easily seen how the contraction diminishes the diameters of the circles of diffusion to *c′ d′* and *c″ d″* respectively.

If the pupil be replaced by two small openings, if, *e.g.*, a card which has been perforated in two places by a pin, be placed in front of the eye, the distance between the perforations being smaller than the diameter of the pupil, two smaller luminous cones are as it were cut out of the larger one, and instead of one 'circle of diffusion' being formed upon the retina, there are two smaller.

In Fig. 20 let *e* and *f* be the holes in the card which replace the pupil; the two luminous cones reunite at B; the retina, if it is not situated in the plane *r r*, but in two planes *r′ r′* or *r″ r″*, receives, instead of the luminous point B, two circles of diffused light *e′* and *f′* or *e″* and *f″* respectively.

All objects which are so placed in reference to the eye, as to throw a diffused image upon the retina, would in the case just considered throw two diffused images, and therefore be seen double (Scheiner's experiment).

Fig. 20.
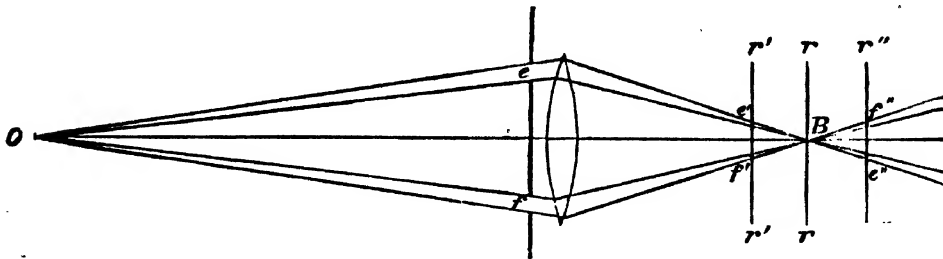
Accommodation.

Daily experience, however, teaches us that a normal eye is capable of seeing objects distinctly which are placed at almost any distance ; there must therefore exist an arrangement, capable of altering the eye, and dependent upon the will. The changes in the eye which occur as a result of this arrangement are included under the term *accommodation*. It is not known with certainty for what distance the eye is adjusted when it is not actively accommodated. It was formerly supposed that the eye when at rest was accommodated for a medium distance, and accommodation was therefore supposed to occur in two directions, in one direction for near objects (positive accommodation), and in another for distant objects (negative accommodation). Now, however, it is almost universally supposed that the normal eye when at rest is adjusted for infinite distances, *i.e.* that the focal point of the normal passive eye lies on the retina. It follows from this that accommodation only occurs in one direction, *i.e.* for near objects.

The principal grounds upon which this view is based are : 1. When the eyelids which have been long closed are suddenly opened, the eye is found to be adjusted for distant objects (Volkmann). 2. The vision of distant objects, unlike the vision of near objects, is not accompanied by a feeling of exertion. (3) Atropia, which paralyses the apparatus concerned in accommodation, causes an unchangeable adjustment for objects which are as distant as possible from the eye ; if a negative apparatus for accommodation did exist, one would have to make the improbable assumption that under these circumstances it was thrown into a state of tetanic activity at the same time that paralysis of positive accommodation occurred (Donders). 4. Even in cases of neurotic paralysis of the apparatus of accommodation (as when the third nerve is paralysed) the eye is always accommodated for infinite distance,

whilst no paralytic condition is known in which the eye is accommodated for near objects.

Accommodation might depend upon the following changes occurring in the eye. 1. Changes in the indices of refraction of the media of the eye. 2. Displacement of the surface of projection (retina), analogous to the artificial accommodation in the *camera obscura.* 3. Alterations in the forms of the refracting surfaces. It is self-evident that the first changes do not occur. A displacement of the retina in the direction of the optic axis would be possible by a lateral compression of the eyeball brought about by the *recti* muscles of the eye; this influence, which was formerly assumed in order to explain accommodation, must be unimportant, seeing that even in eyes which have been cut out of the body changes of accommodation can be occasioned. Changes in the *form* of the refracting surfaces must, therefore, be possible. These have actually been discovered, and they have been found to occur in the crystalline lens.

When the eye is accommodated for near objects, the anterior surface of the lens becomes more strongly curved, and approaches closer to the cornea ; this is especially the case with that portion which is not covered by the iris, and which arches forwards through the pupil (Cramer).

These changes are proved by the following experiment :—

If a lighted candle be placed at one side of the eye, and if one looks into the eye from the other side, three distinct little images of the flame are seen, which are due to reflexion from the refracting surfaces of the eye: the first, erect (virtual), is formed by the anterior surface of the cornea ; the second, which is also erect, but much weaker, is formed by the anterior surface of the lens; the third is brilliant, inverted (real), and is formed by the posterior surface of the lens. If the eye now looks fixedly at an object close to it, the second image becomes perceptibly smaller, and approaches somewhat the first image, affording a proof that the anterior surface of the lens becomes more strongly convex and moves forwards.

Changes of an opposite character occur when the eye stares into infinite distance (Purkinje and Sanson's experiment, Cramer). Instead of a flame it is more convenient to employ one or two luminous points (holes in a screen); the distance between the reflected images of these points can then more easily be measured by means of the ophthalmometer than the size of the image of a flame (Helmholtz).

The protrusion of the iris, which is brought about by an increase in the curvature of the anterior surface of the lens, may be shown in the following way : the caustic line (due to refraction through the corneal surface), which shows itself upon the opposite half of the iris when the eye is

lighted up from the side, changes when the eye is accommodated for near objects then approaching the margin (Helmholtz).

The following table (Helmholtz) exhibits the changes in the optical constants of the eye which occur during accommodation; the places are calculated from the convexity of the cornea, and are reckoned from behind as positive, from the front as negative. The numbers for the condition of rest have been given at pages 357 and 366, slightly modified from those given by Listing for the typical eye.

	Eye at rest : adjusted for distant view	Eye accommodated : adjusted for near view
Radius of curvature of the cornea . .	8	8
„ „ „ anterior surface of the lens	10	6
„ „ „ posterior surface of the lens	6	5·5
Position of anterior surface of the lens	3·6	3·2
„ posterior „ „	7·2	7·2
„ first principal point . .	1·9403	2·0330
„ second „ „ . .	2·3563	2·4919
„ first nodal „ . .	6·957	6·515
„ second „ „ . .	7·373	6·974
„ first focal „. . .	−12·918	−11·241
., second „ „ . .	22·231	20·248
First focal distance	14·858	13·274
Second „ „	19·875	17·756

Accommodation is chiefly effected by the ciliary muscle (M. ciliaris, M. tensor choroideæ, Brücke's muscle). This muscle is composed of both radiating and circular fibres. The first, which constitute the chief part of the muscle, arise from the point of reflexion of the membrane of Descemet, where it passes from the cornea to the iris (lig. iridis pectinatum), and are inserted into the ciliary processes of the choroid; the unimportant circular fibres, which are situated on the inner side of the radiating fibres in the most anterior part of these muscles, surround the border of the crystalline lens. The radiating fibres pull forwards the anterior border of the choroid coat, and so draw the choroid and the retina together like a bag, around the vitreous body (whereby the latter presses the lens forwards). The *zonule* of *Zinn*, the tension of which during the state of rest draws the border of the lens backwards and outwards, and thus flattens the lens, becomes relaxed owing to its posterior insertion being approximated to its anterior (the border of the lens), and thus causes the lens to become thicker (less flat). (Helmholtz.)

The circular fibres appear to co-operate by drawing the ciliary processes inwards, and thus leading to a relaxation of the zonule of Zinn (F. E. Schulze).

The iris also takes a part in the accommodation of the eye for near vision. On the one hand, the part which it plays is passive, in that it assumes a more arched form merely as a result of the greater convexity of the anterior surface of the lens, for the border of the pupil lies immediately in contact with the capsule of the lens;[1] on the other hand, it plays an active part, by the contraction of the pupils. (For the movements of the iris see below.) The contraction of the pupil does not appear to be indispensable to accommodation, seeing that the latter is possible when the iris is wanting or imperfect. Its significance in accommodation is probably to be sought for in the fact that when a lens becomes more convex its spherical aberration increases, and consequently a greater number of the marginal rays require to be screened off. The independence of contraction of the pupil and accommodation is also proved by the fact that the latter precedes the former (Donders).

The nerve fibres which are concerned in accommodation are contained in the ciliary nerves; when these are irritated the eye is accommodated for near vision (Völckers and Hensen). It is in the highest degree probable that these fibres are derived from the third nerve (motor oculi).

Fig. 21 exhibits a section of the anterior segment of the eye; on the left-hand side the eye is shown adjusted for distant vision, on the right for near vision (after Helmholtz).

Concordant data are yet wanting concerning the rate at which the act of accommodation proceeds; the rate is, however, tolerably slow. The change from the state of activity to that of rest occurs more rapidly than the reverse (Hensen and Völckers).

There appears to exist a yet imperfectly investigated central connexion between the nerves which are concerned in accommodation, and those which supply the iris and the external muscles of the eyeball. In favour of such a connexion the following facts may be cited :—1. The behaviour of the pupil in accommodation (see above). 2. Rotation of the eyeball inwards is associated with contraction of the pupil and involuntary accommodation for near vision (Czermak). 3. Atropia, which dilates the pupil, paralyses at the same

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[1] The proof of this statement is afforded by the fact that no shadow of the iris falls upon the lens (Helmholtz); nevertheless only the margins of the iris are in contact with the lens, for between the other parts of the iris and the lens there exists a posterior chamber filled with fluid (Hensen and Völckers).

time, as has been already stated, the accommodating mechanism; conversely Calabar bean occasions contraction of the pupil and tetanic accommodation for near view.

According to some writers, the movements of accommodation always follow a parallel course in the two eyes; others dispute this statement.

For every eye there are definite limits of clear vision; the furthest point, the image of which can fall exactly upon the retina, is called the '*far-point*' (punctum remotum); the nearest point is called the '*near-point*;' the distance between them is called the *region of distinct vision*. In the case of normal

FIG. 22.
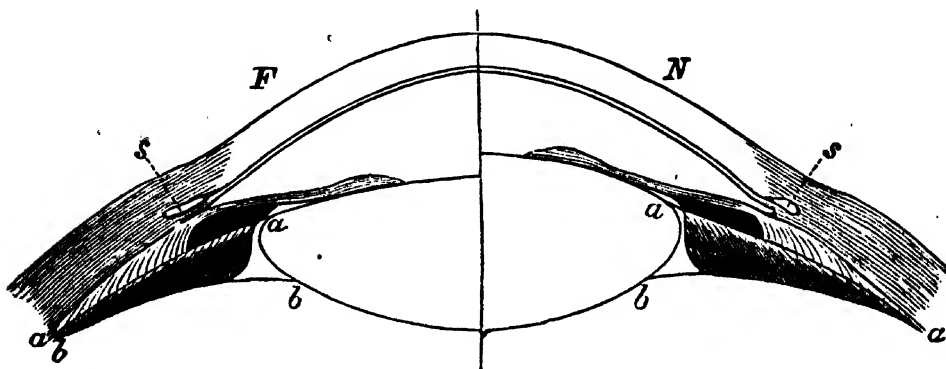
s s, canal of Schlemm; *a a b b*, the folds of the zonule of Zinn, which are intercalated between the ciliary processes; the latter are partly hidden and covered by the former (the section is so arranged that a fold of the zonule lies in front of the ciliary process). The radiating fibres of the ciliary muscle are seen springing from *s*.

eyes the 'far-point' is infinitely distant; the 'near-point,' which is nearer the eye the more active the apparatus of accommodation, is at a distance of between 0·2 to 0·3^{mm} from the eye.

In many eyes which are otherwise normal, the focus during rest does not, as usual (in the *Emmetropic* eye), fall upon the retina, but in consequence of an abnormal length or shortness of the optic axis, it either falls in front of the retina (*Myopia*) or behind it (*Hypermetropia*). The *distant point* of myopic eyes therefore lies abnormally near, the distant point of hypermetropic eyes, on the contrary, is more than infinitely distant —*i.e.* in order to perceive objects which are at an infinite distance the hypermetropic eye must perform movements of accommodation. The activity of the accommodating mechanism

being the same, the near point of the myopic eye must be abnormally near, that of the hypermetropic eye must be abnormally distant. Hence myopic eyes are 'short-sighted,' and hypermetropic eyes 'long-sighted.' Other abnormalities depend upon a small degree of activity of the accommodating mechanism; these naturally only exert an influence upon the situation of the point of near sight, not upon that of distant vision.

The defective or excessive refraction of abnormal eyes—*i.e.*, the relatively too great or too small curvature of their lens, can be corrected by glasses (spectacles); these must naturally, in the first case (in Myopia), be concave; in the second (in Hypermetropia) be convex.

Even deficiency in the power of accommodation may be corrected by artificial accommodation, by means of the temporary use of spectacles. The simplest method of determining the situation of the near and distant point is by ascertaining at what distances the eye can readily recognise distinctly an object which is brought near to or which is removed from it, as, *e.g.*, at what distance letters can be read. This method is, nevertheless, inexact, because the diminution of the *visual* angle by distance makes the object less easily recognisable. A much better method consists in determining at what distance an object throws a clear, and at what distance a diffused, image on the retina. For this purpose Scheiner's experiment (p. 371) affords the best means of investigation. If an object (*e.g.* a pin's head) be looked at through two holes in a card placed close to one another, it appears single if the eye be accurately adjusted, but under opposite circumstances it appears double. If the object be brought closer to the eye, or, on the contrary, removed from it, the space in which it is clearly seen is the field of distinct vision. On this property are based various apparatuses which are used in selecting spectacle-glasses—so-called '*optometers*.' In the best known optometer (Stampfer's) the object is an illuminated slit, the distance of which from the eye can be altered and measured at the same time. As age increases, even after the fifteenth year (MacGillavry), the capability of accommodating for near objects diminishes, presumably in consequence of an induration of the lens (Donders).

Iris and Pupil.

The iris with its central aperture, the pupil, serves at once as a diaphragm to shut off the marginal rays (being thus analogous to the *diaphragms* of optical instruments), as well as to regulate the amount of light entering the eye, and as an auxiliary to accommodation. The size of the pupil depends upon the state of contraction of the two antagonistic sets of muscular fibres in the iris, the sphincter and dilator fibres of the pupil. The first form a circular layer around the pupil, the second have a radiate arrangement; the first derive their nervous

supply from the motor oculi, the second from the sympathetic. If both sets of fibres or their nerves are subjected to the same stimulus, the sphincter fibres predominate and the pupil contracts. Usually both nerves are in a certain state of excitation (tonus), for when one is cut through, the muscle governed by the other predominates. If the cervical sympathetic be divided the pupil contracts ; if the third nerve be divided it dilates.

Recently the existence of a dilator of the pupil has been denied in mammals (Grünhagen, Hampeln). The older view is supported by nearly all the statements of anatomists (lately Henle, Merkel, Dogiel and v. Hüttenbrenner) ; by the dilatation of the pupil when the sympathetic is irritated (those who deny the existence of dilating fibres maintain that this dilatation is a vaso-motor effect) ; and, lastly, by the circumstance that direct excitation of the border of the iris is able to cause local circumscribed dilatation (Bernstein and Dogiel, Engelhardt).

The fibres of the *motor oculi* which cause contraction of the pupil pass to the eye through the *ciliary ganglion* ; this is, however, not the case with the fibres of the *sympathetic* which cause dilatation of the pupil. The latter take their origin first of all in the spinal cord, in the neighbourhood of the lower cervical and superior dorsal vertebræ (cilio-spinal centre of Budge). In pathological conditions, when this region is irritated, the pupil dilates. The real centre for these fibres is, however, situated in the higher regions of the cord, presumably in the medulla oblongata (Salkowski).

In the head the fibres which dilate the pupil run in the course of the trigeminus, the irritation of which occasions dilatation, and the section of which prevents the effect which follows irritation of the sympathetic.

Seeing, however, that after division of the sympathetic the pupil does not contract so powerfully as after the division of the fifth, we must conclude that the fifth contains special fibres capable of dilating the pupil. The origin of these fibres can, in frogs, be traced to the Gasserian ganglion (Oehl, Rosenthal, Hirschmann, S. Guttmann). There exist, however, opposite statements concerning the influence of the fifth pair on the pupil (Rogow).

Movements of the iris occur principally under the following circumstances :

1. *Irritation of the optic nerve occasions contraction of the pupil,* by irritating in a reflex manner the motor oculi. The pupil contracts, therefore, when light falls into the eye, and the more strongly, the more powerful the light. In this way the amount of light which reaches the retina is partly regulated. Con-

traction of the pupil also occurs when the trunk of the optic nerve is irritated (Mayo), and ceases after division of the *motor oculi*. Irritation of one optic nerve is sufficient to cause contraction of both pupils. Generally both pupils are, under normal circumstances, of the same size (Donders).

2. *When the eye is accommodated for near vision the pupil contracts.* Poisons which occasion tetanic accommodation for near vision (Calabar bean) also cause contraction. This contraction is caused by an excitation of the nerves which contract the pupil, and is to be looked upon as a kind of ' associated' movement (Chap. XI.). This contraction commences later, and (in the toxic form) disappears earlier, than the affec tion of accommodation, and is therefore only partly dependent upon the latter.

The contraction of the pupil which is caused by light commences, on an average, about 0·49 sec. (0·4 Listing) after the irritation, and the maximum effect (contraction) occurs 0·58 sec. after the irritation.

The contraction connected with accommodation begins 0·41 sec., and reaches its maximum 1·13 sec. after the cause which occasions it. The dilatation which follows irritation of the sympathetic commences in rabbits 0·89 sec., and reaches its maximum 3·40 sec. after the commencement of the irritation (Arlt, jun.)

3. *Rotation of the eyeball inwards occasions* a *contraction of the pupil,* as a kind of ' associated' movement, by irritation of the motor oculi.

As the eyes are during sleep turned inwards and upwards, the contraction of the pupils which is observed during sleep can be explained.

4. *During dyspnœa the pupils are dilated;* this dilatation ceases when asphyxia sets in. This dilatation depends upon irritation of the centre which exists in the cord and which presides over the pupil, for it does not occur if the sympathetics have been previously divided.

5. *Powerful irritation of sensory nerves causes,* in a reflex manner, *dilatation of the pupil* (Bernard, Westphal).

6. *Violent muscular efforts* (especially powerful inspiratory and expiratory movements) *are associated with dilatation of the pupil* (Romain-Vigouroux).

In addition, in the normal state, a very slight alteration of the pupil is observed to occur with every beat of the pulse, as well as with every ex-

piration; every flow of blood to the iris appears especially to occasion a contraction of the iris; in this way may be explained the contraction of the pupil which follows withdrawal of the aqueous humour (Hensen and Völckers).

7. Numerous poisons, either when introduced into the blood or topically applied, induce changes in the size of the pupil. Atropia, for example, dilates the pupil, by causing a paralysis of the terminations of the third nerve in the circular fibres of the iris. Nicotia, physostigma, morphia, &c. cause contraction of the pupil (*Myosis*). This is due, according to some, to a paralysis of the terminations of the sympathetic in the dilating (radiating) fibres, but, according to others (Grünhagen), to irritation of the third nerve. Anæsthetic poisons (chloroform, alcohol, &c.) occasion in the first place a contraction, and afterwards a dilatation of the pupil.

The kind of action which these poisons exert is still matter for controversy. Meanwhile the supposition that they all exert an action upon the sphincter arrangement of the iris appears the most probable, seeing that the poisons under dispute exert a simultaneous and corresponding action on the apparatus engaged in accommodation. It is especially a matter of doubt whether the poisons which induce contraction (Myotics) act by paralysing the sympathetic; in support of the latter view it is stated that irritation of the sympathetic does not exert any action upon the pupil of animals under the influence of such poisons; this result might be due to the intensity of the tetanic contraction of the sphincter fibres.

Further, the circumstance that the action of atropia manifests itself even after division of the ciliary ganglion (Hensen and Völckers), and that the action of these poisons occurs when they are dropped into the eye, render it very probable that yet unknown ganglionic centres exist either in the iris itself, or in its immediate proximity (v. Bezold).

When one pupil is dilated by atropia, the other contracts and remains contracted in consequence of the large amount of light which falls into the first eye.

Anomalies and Peculiarities of the Eye.

From what has been stated in the preceding pages it is seen that a sharp, diminished, and inverted image of any object brought within the field of distinct vision can be formed on the retina. Yet the absolutely faultless production of such images is rendered impossible in consequence of certain properties of the eye, which it shares with other optical instruments: these are—

1. *Chromatic Aberration.* White light, as is well known, is decomposed by refraction into its coloured components, in consequence of the unequal refrangibility of the latter. Consequently, if white light proceeds from a point in an object, the latter, instead of having a single spot corresponding to

it in the image, must have a series of such points lying one behind the other, the most anterior point corresponding to the most refrangible (violet), and the most posterior to the least refrangible (red) rays. The eye cannot therefore be thoroughly accommodated for a white object: if, for instance, it is so accommodated that the image of the violet rays falls upon the retina, the remaining colours appear in concentric diffusion-rings, which are larger the further the colour is separated from violet; as, however, all the diffused rings and the violet spot fall on the middle, there results a white spot with coloured borders. Similarly every white object must appear white with coloured borders as the coloured diffused images are superimposed as far as the margins.

If the eye be accommodated for a colour which lies in the middle of the spectrum, as for green, there result, naturally, two series of coloured diffused images; these cover one another to such an extent to the very borders that the *complementary colours* (see below) fall upon one another, and the borders even appear in great part to be white. The latter circumstance is one cause why in ordinary vision we do not see the coloured borders of the objects which are looked at; these coloured borders, moreover, in consequence of the slight dispersive power of the media of the eye (the dispersive power of which is nearly the same as that of distilled water), are very slight, and disappear entirely when contrasted with the powerful white light which falls upon the middle of the eye : possibly, too, the combination of the different ocular media tends to make the eye achromatic (the arrangement being analogous to the combination of flint and crown-glass lenses in optical instruments). In order clearly to perceive these coloured margins, the eye must be accommodated, not for a colour in the middle of the spectrum, but for a colour at the extreme end (red or violet); this is obviously best done by not accommodating for the object.

White fields appear, when the eye is accommodated for too great a distance, to possess a faint reddish yellow margin ; when the eye is accommodated for too near a distance the margin is blue (Helmholtz) ; a luminous point seen through a reddish-violet glass appears, when the eye is accommodated for the red rays, to be red with a violet circle of diffusion ; in other cases the converse occurs (Helmholtz). From what has been stated it also results that the extent of the field of distinct vision is various for these different colours. Naturally the point of near and distant vision for violet light must be appreciably nearer than for red, a fact which can be proved by looking through a telescope at equally distant spots of various colours, when the glass must be adjusted differently in order that all the colours should be seen with equal distinctness (Frauenhofer).

Red surfaces appear nearer than blue surfaces which are in the same plane, because the eye has to be more strongly accommodated for the former, and therefore judges the object to be nearer (Brücke).

2. *Spherical (monochromatic) Aberration.*—As has been already frequently stated, the rays which proceed from the point in an object can only join again to form the point of an image when they fall upon the spherical refracting surface within a very small distance of the axis. This condition is in part satisfied by the iris when it cuts off a large number of the peripheral rays

which fall upon the eye. A further correction is effected by the form of some
of the refracting surfaces of the eye; being *ellipsoids,* their curvature dimin-
ishes decidedly near the margins.   Moreover, in the case of the lens, the rays
which pass through its borders only traverse the outer layers, which possess
smaller powers of refraction than the inner.   This correction is, however,
never perfect, being sometimes not sufficient, sometimes too great, so that
nearly always, especially when the pupil is dilated, a certain amount of
aberration is present, which gives rise to circles of diffused light, and con-
sequently to indistinct images.

Sometimes a defective centering of the refracting surfaces of the eye
can be discovered (Brücke).

Some other forms of monochromatic aberration are the following:—

Astigmatism (Helmholtz, Knapp, Donders).— *a.* So-called 'irregular
astigmatism' depends upon various deviations in the curvatures of the
refracting surfaces, so that the union of a homocentric pencil of rays at one
point is hindered; each small segment of the surface has its special image,
so that an object such as a point throws a star-like (fixed star) image upon
the retina.   The cornea, moreover, is subject to transitory inequalities of its
surface (tears, &c.).   *b.* 'Regular' astigmatism depends upon a difference
of the curvature of the refracting surfaces in different meridians.   The two
meridians which are furthest removed from one another are called principal
meridians.   As a rule, the vertical meridian is more arched than the
horizontal.   The two meridians, therefore, possess different focal distances,
so that the eye may be short-sighted in the vertical meridian, and long-
sighted in the horizontal.   Generally, however, the difference is so slight
that it can only be discovered by looking at fine parallel lines from a
distance; these can be seen from a greater distance, when vertical than
horizontal.   When the degree of astigmatism is very great, it is corrected
by a glass which is stronger in one direction than the other, or, more simply,
which is only curved in one direction, which is, therefore, *cylindrical.*

3. *Fluorescence.*—All the media of the eye are fluorescent; the lens is
most so (Helmholtz, Setschenow, Regnauld).   As the sensitiveness of the
retina is restricted so as to permit of its only appreciating waves of a
certain length, the fluorescent property of the media tends to increase the
range of perception for light of smallest wave-length (ultra-violet rays).
Of the true limits more will be said below.

4. *Polarization.*—If polarized blue light, or light which contains blue,
falls on the eye (for example, if we look at the sky through a Nicol's prism,
or even with the naked eye, as the blue rays of the sky are already polarized),
a tuft-like image (Haidinger) is seen, which moves with the eye.   The powers
of double refraction which the ocular nerves possess (Janin, Valentin) are
not sufficient to explain this phenomenon.   It appears to depend upon the
(presumably doubly refracting) fibres of the yellow spot (see below), which
being struck by the polarized light at different angles, absorbs at one place
more, at another less, giving rise to the appearance above mentioned (Helm-
holtz).

On the behaviour of Light which penetrates the Eye.

The luminous rays after penetrating the eye are in part absorbed and in part reflected, so that issuing from the eye they follow the same course which they pursued on entering. Each bundle of homocentric rays entering an eye which is perfectly accommodated is, after refraction, brought to a focus on one point in the transparent retina, presumably on its outer layer (of rods and cones). Each rod [1] is to be looked upon as a prism of very high refractive power the base of which touches the choroid, and which at its margin lies in contact with a feebly refracting *intermediate substance* (Brücke). The rays which, after uniting to form points in the image, again diverge, come in part in direct contact with the choroid (axial rays) and in part strike the sides of the rods, but at so oblique an angle, that instead of being refracted by the *intermediate substance*, they undergo *total reflection*. Ultimately all these rays must be thrown upon the choroid. Here they are almost all absorbed by the black pigment; the unabsorbed rays, however, are reflected, in part directly (axial rays), in part after reflection from the sides of the rods. According to well-known optical principles, they ultimately return again to the point in the object from which they emanated. By this arrangement the passage of rays from one part of the retina to the other (phenomena of interference, &c.) is avoided, and clear vision is made possible. Upon this arrangement, too, depends the fact that on looking into the eye the fundus always appears dark.

In order to see the fundus of the eye illuminated, the observer must make his own retina the point of departure of rays which are perceived on their return from the observed eye. This object is attained by the use of the *ophthalmoscope*. By means of this instrument the light of a flame is thrown into the eye as if it came from the eye of the observer.

One of the simplest ophthalmoscopes (Helmholtz's) consists of an arrangement of glass plates, which serves at once as a mirror and as a transparent medium. By means of this arrangement of plates the luminous rays from a light placed at the side of the observed eye are thrown into the latter. The rays which return

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[1] According to recent researches it is only the external segments of the rods or of the analogous cones which have this function.

after reflection from the fundus are only in part thrown back by the plates to the source whence they first emanated (the light); in part they traverse the plates and reach the eye of the observer. The observed eye appears in this way to be diffusely illuminated with a red light.

A clear image of the fundus of the eye may further be obtained in the following manner. When the observed eye is placed at an infinite distance, the retina is somewhat behind the focal point of the optical system, which, like the object-glass of a microscope, throws a real, inverted, and enlarged image of the retina in that plane to which the eye is turned. As this image, in consequence of its large size (which only permits of a small part of it falling at once upon the pupil of the observer), and on account of its continually changing position, cannot be observed, an auxiliary lens must be employed: this is either a collecting convex lens, which makes the image smaller, brighter, and brings it nearer to the observer, whilst it allows it easily to be fixed in one place, or it is a concave lens, which possesses similar properties, but which furnishes a distinct and erect image.

The combination of glass plate in the instrument above referred to may be replaced by a plane or concave mirror; which, being furnished with a central aperture, permits a portion of the rays returning from the fundus of the observed to reach the observing eye; upon this plan other ophthalmoscopes have been constructed (those of von Ruete and Coccius). Between the source of light and the (plane) mirror, a convex lens may be placed with the view of concentrating the rays. If it be desired merely to see the eye diffusely lighted up, and not to obtain a sharp image of the retina, the following procedure may be had recourse to (Brücke). The eye which is to be observed is fixed upon a near luminous object, but is accommodated for distant vision. Instead of the rays of light then converging to points, circles of diffused light are formed upon the retina. The reflected rays which leave the eye under these circumstances do not again meet at the points whence they emanated, but either far behind them or they do not meet at all (*i.e.* they are either parallel or divergent). If now the observer's eye is placed in the path of the cone of the returning rays (being protected, if needs be, from the direct influence of the flame by a screen), the observed eye is seen to be illuminated, of a red tint.

The eyes of human and animal albinos exhibit, without any special arrangement being required, an illuminated fundus, as light passes through the sclerotic and choroid, and falls into the eye. The illumination of the eye is especially brilliant in animals, in which over a portion of the choroid the black pigment is replaced by a bright, shining, strongly reflecting membrane, the so-called *tapetum* (this is seen in the eyes of many of the *mammals*, especially in beasts of prey, and cetacea, in fishes, &c.).

Vision.

The rays which fall upon the retina lead to the perception of light, in consequence of the vibrations of the ether affecting in an unknown manner the terminations of the optic nerve in the retina.

The only nerve terminations which are to be considered sensitive to light are *the rods* and *the cones*. The proofs for this statement are the following :

1. The point of entrance of the optic nerve, where the retina consists of nerve fibres without either rods or cones, is insensitive to light ; this is therefore called *the blind spot* (also Mariotte's spot). If we look fixedly with the right eye at the spot A (keeping the left eye closed), holding the paper at a

A   B

●   ●

distance from our eye four times as great as the distance of A from B, the point B will not be seen. In this case, by looking at A, its image falls upon the termination of the optic axis, and the image of B falls upon the point of entrance of the optic nerve, which is situated about $3\frac{1}{2}^{mm}$ on the inner side. Likewise A disappears, if B be looked at fixedly with the left eye at the same distance as in the previous experiment. The function of the blind spot in the field of vision will be discussed below.

2. The *fovea centralis retinæ* and the *macula lutea* which surrounds it, which contain rods and cones, but no fibres of the optic nerve, are fitted for the most acute vision (the fovea centralis almost exactly coincides with the termination of the optic axis); the image of any fixed object which is looked at falls upon this part of the retina. As the fovea centralis only contains cones, and the macula lutea cones in large numbers (one cone being surrounded by a circle of rods), and as the remaining part of the retina contains only few cones (one cone surrounded by many circles of rods), we are entitled to conclude that the cones are even more sensitive to light than the rods.

3. When the eye is illuminated from without, the vessels of the retina which are situated behind the layer of fibres, but anterior to the layer of rods and cones, cast a shadow ; as this

shadow can be perceived *entoptically*, under certain circumstances which will have to be discussed (Purkinje's figures), it is proved that the rods and cones are the structures which are sensitive to light. By accurate measurement it has been determined that the shadows which are perceived really are shadows of the blood-vessels of the retina, and not of other vessels situated in front. For example, by moving the source of light, the position of the shadow changes, and as these changes of position can be measured entoptically, the distance of the bodies which cast the shadows from the sensitive surface can easily be calculated. The distance agrees exactly with the distance between the vessels of the retina and the rods, as ascertained by direct measurement (H. Müller).

The end-organs, the rods and the cones, are, therefore, the only organs which are directly capable of being excited by the vibrations of the ether ; this property not being shared by the fibres of the optic nerve either in the retina or in the trunk of the nerve. Irritation of the optic nerve, at any point in its course or terminations, by any of the usual nerve excitants (mechanical, electrical, &c.) gives rise to the sensation of light, which, therefore, constitutes the ' specific energy ' of the optic nerve.

Mechanical irritation, as contusion or section of the trunk of the optic nerve, leads to a lightning-like illumination of the whole field of vision. Pressure applied to the eye or to a limited part of the retina leads to circular bright ' pressure-figures,' ' phosphenes,' upon the corresponding (opposite) side of the field of view ; in eyes which are morbidly excitable, the contact of the circulating blood with the retina is sufficient to occasion manifestations of light (sparks, images of the vessels); lastly, a sudden change in the accommodation of the eye in the dark, by causing a traction upon the anterior margin of the retina, gives rise to the appearance of a bright fringe at the border of the field of view (Purkinje, Czermak). Electrical irritation (passage of a constant current through the eye, or variations in the intensity of the current) also occasions peculiar appearances of light, different parts of the retina being perceived (Ritter, Purkinje). For the influence of electrical irritation upon the perception of colour, see below.

In order to bring about an excitation of the retina the luminous impression need only act upon it for a very short period (the time of duration of an electric spark suffices). When light continues to act upon the retina for a long time, the excitation becoming more intense, fatigue of the retina results. These facts explain the following : 1. The appearance of persistent ' negative images ' (see below). 2. The much greater

sensitiveness of the retina after the eye has been in darkness for considerable periods. 3. The greater effect produced by intermittent luminous stimulations as compared with those which are continuous. The effect of such intermittent stimulations is most marked when they follow one another seventeen or eighteen times in each second (Brücke), presumably because then the new irritation exerts its influence at a time when the eye has just recovered from the effect of the preceding; the complementary after-images (see below) co-operate in bringing about this effect (Brücke).

A much shorter time suffices for the perception of yellow than for that of violet (Vierordt, Burckhardt and Faber); red requires the longest time (Lamansky); the intensity of light required for perception is nearly the same for all colours.

The brighter and larger the images which are formed on the retina, the shorter is the time necessary for their perception, yet the time required only diminishes in arithmetical, though the intensity of the illumination and the size of the retinal image increase in geometrical, progression. The most sensitive part of the retina lies further from the centre of the retina than that part which perceives most rapidly the outlines of objects (Exner). The curve which represents the excitation of the retina presents a rise and a fall, so that when the illumination lasts a very short time, the full perception of the luminous impression does not occur (Fick). When the eye is continuously illuminated, the falling part of the curve indicates exhaustion of the retina. The absolute brightness of the light has no influence on the relative fatigue; the effect of this fatigue is the same as if the objective light were diminished in intensity by a fraction of its whole amount (Helmholtz). Fatigue increases most rapidly at first; the loss of light due to fatigue amounts in the first seconds, during which the luminous impression lasts, to more than 7 per cent. of the total amount; later, however, the loss is relatively much less. The whole loss during exposure for a whole day amounts to about 51 per cent., because the eye has continuous opportunities for restoration. In the morning the influence of fatigue is greatest (Fick, and C. F. Müller). In the centre of the retina the influence of fatigue is sooner developed than at the periphery (Aubert).

Quality of Luminous Impressions.

All the vibrations of the ether do not possess the power of exciting the end-organs of the optic nerve. Those the wavelength of which is greater than corresponds to Fraunhofer's line A (ultra-red heat rays) are unable to excite them, and are, therefore, invisible; those the wave-length of which is shorter than corresponds to the line H (ultra-violet chemical rays) exert so

feeble an action that peculiar arrangements are required in order to make them manifest.

The invisible character of the ultra-red rays has led to the investigation of the *diathermancy* of the media of the eye, and it results that the latter absorbs above 90 per cent. of the heat rays (Brücke, Janssen). In relation to the separate portions of the spectrum, the diathermancy of the media of the eye behaves as that of water (Franz); they therefore allow a sufficient number of the ultra-red rays to pass, to lead one to ascribe their not being perceived to their incapability of exciting the retina. The ultra-violet rays, which are seen with difficulty, appear of a lavender grey colour when they have been rendered artificially visible by removing the remaining portions of the spectrum (Helmholtz); the most external rays of the very long spectra of metals have no perceptible colour (Masoart).

The vibrations of the ether which are capable of exciting the retina give rise to the sensation of light by being propagated from the end-organs in the retina to the central organs in connection with the optic nerve.

The *intensity* (height of wave) of the waves determines the intensity of the luminous impression; the length of the waves, however, determines the specific peculiarities of the luminous impressions, to which we give the name of *colours*. The solar spectrum, which allows rays of all wave-lengths capable of affecting the eye to reach it simultaneously, exhibits all colours arranged side by side. In addition to these, which we denominate 'simple,' there are others which we term 'mixed' colours. The consciousness of the impression produced by a mixed colour is the result either of the union of rays of different wave-length (different simple colours), which have united so as to form a resulting wave-system which strikes the retina; or of a simultaneous excitation of corresponding fibres of the optic nerve by several rays of different colour.

In both cases the same simple colours give rise to the same mixed colour.

The sensation produced by the absence of any luminous impression upon a part of the retina which is sensitive to light is called 'black.'

We may realise the two modes in which colours are mixed in the following manner: 1. Formation of a system of waves of different wave-lengths. *a.* The source of light itself furnishes such a system, which is decomposable by a prism into simple colours. *b.* The same effect results when luminous rays proceeding from several points strike the eye so as to fall upon the same spot in the retina. Simple means of effecting this are the following:

a colour is looked at through an obliquely-placed glass plate, which at the same time throws, by reflexion, another colour into the eye (Helmholtz), or, in Scheiner's experiment, which was previously referred to, two differently coloured glasses are placed in front of the two small apertures; in this case the two luminous cones are differently coloured. If the observing eye be now so accommodated that the two circles of diffusion partly cover one another, that part of the retina which is common to both is illuminated with a mixed light (Czermak).

2. Excitation of the same or of corresponding elements of the retina by different colours. *a.* The property which the retina possesses of retaining for a time luminous impressions is made use of, and different colours are allowed to fall into the eye in very rapid succession (the apparatus known as Newton's disc is made use of in this experiment); in this way the effect of the first excitation is still present, when the second commences to operate. *b.* Different colours are allowed to fall upon two ' *corresponding points* ' in the two eyes.

Experiments conducted upon the perception of colours and upon mixed colours (Newton, Grassmann, Helmholtz, Maxwell) have led to the following laws : 1. The same impression of colour may be produced by very different combinations of colours; the number of possible colour-perceptions is therefore much smaller than that of the possible objective wave-forms. 2. Each colour appears whiter, the more intense the illumination, and when the illumination is most intense it appears white ; of all colours yellow is the one which most easily passes into a white. 3. A combination of two simple colours of the spectrum gives rise to an impression, which can in every case be reproduced by a colour lying between them in the spectrum, mixed with a certain quantity of white (*i.e.* undecomposed sunlight), or it may be reproduced by white alone (in the latter case the two colours are called *complementary colours*); hence it follows that even three or more colours of the spectrum when mixed always produce an impression, which can be reproduced by one of the colours of the spectrum mixed with white ; any luminous impression whatever may therefore be · produced by one of the colours of the spectrum and white.

In order to make the third law universally applicable, we must consider the spectrum to be in the form of a closed ring, a new colour being interposed between the red and the violet ends, this being a compound colour, viz. *purple,* resulting from the mixture of red and violet. If in the middle of this closed field (Fig. 22) white be placed, and if the field be so coloured, that every *vector* contains the combinations of one of the spectral colours with white in all proportions (so that the colour as it approaches the

white always becomes whiter), a diagram is obtained, which immediately tells us what impression will result when any given colours are mixed. Let us, for example, imagine that at the points which correspond to the coloured components masses are placed, the magnitude of which corresponds to the intensity of the components, and let the centre of gravity of these (which must naturally lie within the field) be found; its situation will

Fig. 22.
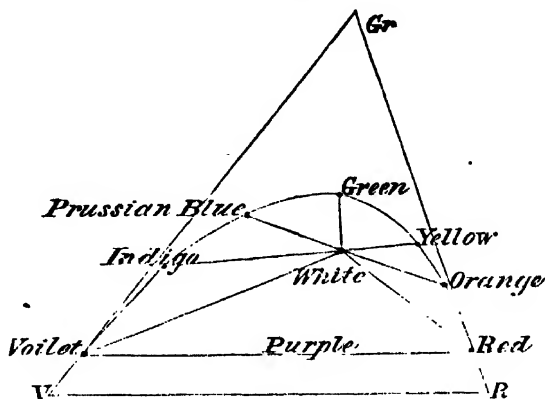
represent the luminous impression sought for. It is then seen that the coloured impression produced by the spectral colours corresponds to a spectral colour which lies between the component (elementary) colours, mixed with white; further, that the mixture with white becomes more intense the more diametrically opposed the two ingredients; lastly, that each shade of white unites two complementary colours.

The form of the including curve and the situation of the white must therefore be so chosen that the latter always lies in the line of union of two complementary colours, and indeed always lies nearer to that colour which must be represented relatively more intensely in order to form white with its complementary colour.

If we supposed that every fibre of the optic nerve were differently excited by different colours and so occasioned different luminous impressions, not only would the principle of 'specific energies' (p. 344) be contradicted, but many of the observations which have been referred to, especially the identity of the impressions perceived when the same colours are mixed objectively and subjectively, would be absolutely incomprehensible. All difficulties, are, on the other hand, set aside by the hypothesis of Thomas Young and Helmholtz, that each spot on the retina contains a number of nerve-terminations, of which each one is capable of being excited by one particular colour and is able, by transmission through a nerve fibre in connection with it, to occasion the consciousness of a particular coloured im-

pression. A compound colour would then be decomposed (just as a musical sound is decomposed by resonators, or like light by a prism) into its components, which would excite the corresponding fibres. Admitting this hypothesis, the same impression would naturally result whether a compound colour, or each of its separate components, fell upon the retina, or if the components fell in rapid succession upon the retina, or even were distributed upon corresponding points of the two retinæ. According to this hypothesis, white would be perceived when all the retinal elements were equally excited.

It is impossible to determine *a priori* how many of these colour-perceiving retinal elements must be associated with each spot on the retina ; the smallest number which can be assumed is three (Young). For reasons which cannot here be discussed, it is usually assumed that there must be present elements capable of perceiving red, green, and violet. Probably the number is actually much greater.

The most recent anatomical investigations have almost certainly demonstrated, that the *cones* are the elements in the retina which are concerned in the perception of colour (M. Schultze). These *cones* must, however, be looked upon as collections of nerve terminations ; they appear to be longitudinally striated, and they pass into a thick fibre (cone-fibre), which consists of a bundle of the finest axis cylinders, which separate in the granular layers of the retina. The power of perceiving colours possessed by different parts of the retina varies according to the distribution of cones in them. The rods are in all probability merely endowed with the power of determining the quantity of light. They are connected with a single axis cylinder, or at least with a far smaller number of axis cylinders than the cones.

The hypothesis which has already been referred to in the text, viz. that each of the fibres supposed by Young to exist, is excited not merely by one, but by all colours, only in different degrees, explains the observation referred to at p. 389 in discussing the second law. In Fig. 23 the ordinates of the curves indicate the relative degree of stimulation which each of Young's fibres undergoes under the influence of each of the primary colours of the spectrum. 1 is the curve which represents the excitability of the fibres which are specially sensitive to red

rays ; 2, of those which are sensitive to green rays ; 3, of those which are sensitive to violet rays.

As when the intensity of the illumination increases, the stimulation must soon attain a maximum, it follows that an intensely illuminated colour must excite all three fibres to a maximum degree, therefore equally strongly, and that therefore a sensation of white must result. Yellow, which, as the curves show, excites almost to an equal degree the three kinds

FIG. 23.
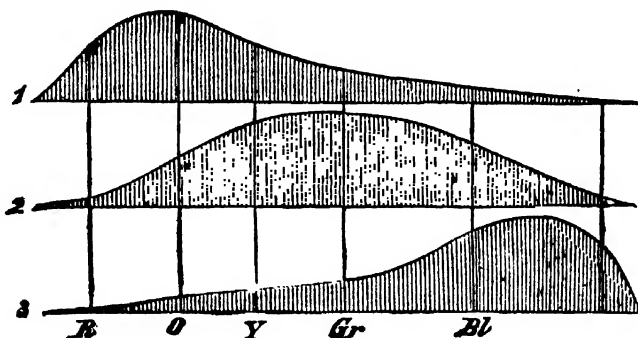
of fibres, must most easily pass into white. In the colour-plane (Fig. 22) places must be given to coloured impressions which correspond to the excitation of the individual fibres of Young, outside of the coloured field, viz. at R, Gr and v; then, as Fig. 23 shows, no objective colour exists, which merely stimulates a single fibre of Young. Naturally again white must lie in the centre of gravity of three equal masses placed at R, Gr and v. The triangle R Gr v includes all *imaginable* coloured impressions, but the inner field alone contains those which are *possible* in the case of objective illumination; the remaining colours can only be developed subjectively.

The theory of Young, Helmholtz and Schultze is moreover supported by the following facts in addition to those previously referred to (viz. the results of mixing colours ; the form of the fibres of the cones and rods) ; 1. In animals the habits of which are nocturnal (owls, bats) the cones are wholly wanting, and rods alone are present (M. Schultze) ; this fact agrees with their supposed function of merely appreciating differences in the quantity of light (light and darkness). 2. The power of descriminating colours is, in the eye of man, most developed in the *fovea centralis*, where cones alone are present, and diminishes towards

the periphery in proportion as rods occur, ceasing entirely *at* the periphery, where the cones only occur in isolated situations (Aubert, M. Schultze). Here a qualitative irregularity in the perception of colours is discovered (see below). 3. Very frequently there exists an abnormality of the eye, to which the name of colour-blindness or blindness for red (Daltonism) is given. This abnormality consists in this, that red appears black, and that mixed colours which contain red appear as if the red were absent (white for instance appears greenish-blue). This condition cannot be explained otherwise than by supposing an absence, or a functional incapacity, of the retinal elements concerned in the perception of red. As some colour-blind people do perceive very intense red, it follows that we must assume not an absence, but an imperfection of these elements, of which there may be many gradations. The peripheral parts of the retina are normally to a certain extent colour-blind for red, and are so, according to Woinow, for green also. White is seen on those parts of the retina of a greenish tint. Moreover, when we try to ascertain the limits of the sensitiveness of the eye to colour, as for example the power of perceiving a very small coloured image or one imperfectly illuminated, red appears to be the colour which is least easily perceived (Aubert, Lamansky); it would thus appear that the cones which are sensitive to red require a stronger stimulus than the remaining cones, and further that in order that a colour be perceived, it is necessary that a certain number of cones be excited; these two suppositions are sufficient to explain all the known phenomena (still even a green colour-blindness can exist, Preyer).

When electrical currents are passed through the optic nerve, weak luminous sensations result; the field of vision appears of a violet colour with an ascending, and reddish-yellow with a descending, current (Ritter). This action manifests itself when coloured objects are looked at, by an addition of violet or yellow to their proper colour.

The excitation of the fibres which are sensitive to violet rays, appears therefore to be stronger with an ascending current, and weaker with a descending current, whereas the fibres which are sensitive to green or red are but slightly affected.

The yellow colouring matter of the *macula lutea* causes

the centre of the retina to be more sensitive for yellow and less sensitive for violet, as many facts teach us (Maxwell, Preyer). The yellow colour of the field of vision, which comes on in cases of poisoning by santonin, has been explained by some (M. Schultze) as due to an increase of the yellow pigment, whilst others (Hüfner) imagine that it depends upon a paralysis of the fibres which are sensitive to violet, especially because, as a first effect, the field of vision is coloured violet—a phenomenon which is to be explained on the supposition that there is a preliminary stage of irritation which precedes the stage of paralysis of the fibres.

The manner in which light of different colours is decomposed in the cones cannot yet be understood (see below). But birds are provided with an apparatus which throws some light upon the function of the cones in the perception of colours. The cones of the retina of birds are simple elements, being only connected with a single, simple axis cylinder, and are therefore, according to Schultze's theory, really *rods :* these rods present, however, at the junction of their inner with their outer segment (see below) a spherical fatty body, which in the case of some is red, in that of others yellow, or even colourless. It is conceivable that the rods of the first kind only transmit red, those of the second yellow, those of the third perhaps white light. The perception of colours appears therefore, even in this case, to depend upon several rods, each kind being excited by light of a particular colour; this combination of rods corresponds to a single cone of the human retina (M. Schultze). In the retina of the owl the pigmented rods, above referred to, are absent, the only ones present being colourless.

In both rods and cones two constituent parts (segments), an inner and an outer, can easily be distinguished (M. Schultze). The external segment is essentially the same in both rods and cones, being merely longer in the former ; it is regularly rod-like, it refracts light strongly, and is most strongly coloured black by perosmic acid ; it constitutes a reflecting arrangement. The internal segment differs in the rods and cones ; in the former it possesses the same thickness as the external part, in the latter it is fusiform and longitudinally striated ; it is apparently of a purely nervous nature. The line of demarcation between these two segments is sharp, and here the rays coming

from within must, in great part, be totally reflected. The light which penetrates the external portion of the rods and cones is either absorbed by the choroid coat or again reflected towards the inner portions. Seeing that in the retina of birds the pigmented granular bodies are situated at the point of junction of the inner and outer segments of the rods and cones (while in other animals also refracting apparatuses of elliptical or lenticular form occur in the same situation), it is highly probable, that the external segments are the specific light-perceiving organs. These present in all animals a transverse cleavage into fine plates, which are $0·0006^{mm}$ thick in doves, and $0·002$—$0·008$ in crabs (M. Schultze). This peculiar structure has led to the hypothesis that the external segments have the property of changing by reflection against these plates the progressive light-waves into stationary waves; the latter would act in such a way that the maximum point would not coincide in the case of the different colours, but that individual colours would excite different points of the organ, an effect similar to that required by Young's theory. That stationary waves corresponding to all the different wave-lengths may be generated appears possible from the fact that not only the distance of the reflecting surfaces (thickness of the plates), but also the refractive index of the different plates in a rod, vary.

Images.

It has already been stated that from every point in an object the corresponding point in the image can be obtained by drawing the visual ray which joins them. It is in this direction too that consciousness refers to the exterior the cause of every luminous impression which originates in consequence of the irritation of a retinal element. It will be shown subsequently to what distance on this line the point of the object is referred. In the first place, let us now consider the case in which the transfer is effected in such a manner that all the points of the object appear to lie in a plane floating before the eye. This plane is called the ' field of vision.' As consciousness is continually forming a representation dependent on the state of irritation of all the retinal elements according to their real arrangement in space, it happens that a *field of*

vision is always being seen; this appears 'black,' as long as every cause of irritation is wanting. To every excited retinal element there corresponds a luminous point, and to every unexcited element a black point, at diametrically opposite points of the field of vision. The latter then is filled with exactly the same, but inverted, images as are objectively present on the retina. As the latter are, in relation to the objects seen, inverted, the objects are seen erect in the field of view.

The blind spot does not occasion any perceptible gap in the field of vision. The want of optical excitation (the consciousness of which we designate by the term black) can only be perceived where terminations of nerves sensitive to light are present. But there are no such terminations in the blind spot. The latter therefore behaves towards light as any spot on the skin would do; we do not experience with the hand any sensation of black, although no luminous impression proceeds from the hand. As the visual impressions of the contour of the blind spot are by means of the visual rays localised in the field of vision, consciousness must logically perceive the want of intermediate luminous points, and appears to conceive them according to the rules of *probability* (E. H. Weber). In this way we may probably explain the experiment described at page 385 in which the place of the object which has disappeared is taken by the colour of the ground and not by a black spot. The white colour of the paper here fills up the gap as the most probable substitute.

As every point in the retina merely contains a definite number of terminations of the optic nerve (rods or cones), any image can only consist of a limited number of luminous impressions separated from one another in space and forming a kind of mosaic or embroidery pattern. But the mosaic is so fine that there may result an impression as of a continuous drawing. The same object must appear sharper, the greater the number of sensitive retinal elements over which its image is distributed. Hence the sharpness with which a given object is perceived depends (1) upon the magnitude of its retinal image; the same object will therefore appear sharper when near than when distant; (2) upon the situation of the retinal image, for the sensitive retinal elements are most thickly pressed together in the *fovea centralis* and the *macula lutea*,

whilst they are most sparsely scattered near the borders of the retina. An object, therefore, which is situated at the same distance will be seen most sharply when its image falls upon the centre of the retina ; hence when the eye looks most keenly at (*i.e.* is fixed upon) an object, it is so turned that the latter throws its image upon the middle of the retina, on the *fovea centralis.* The visual ray which strikes the *fovea centralis*, viz. the axis of vision, does not absolutely coincide with the optic axis of the eye ; but is bent backwards and a little outwards and downwards from the latter. The two form an angle of $3°·5$ —$7°$ with one another.

This deviation of the two axes can be recognised and measured by causing the centre of a horizontally placed measuring rod to be fixed by the eye observed; at one end of the rod is a light, at the other the eye of the observer. The three luminous reflexions which wĕre previously referred to in describing Mariotte's experiment do not then appear in symmetrically similar order if the observer and the light change places; the symmetry is only restored when the observed eye is fixed, not upon the centre, but on a point somewhat to the inner side of the centre, of the measuring rod. The symmetry is even then not absolutely perfect, because the centering of the three refracting surfaces of the eye is not absolutely true.

An object will further not generally be recognisable, unless its retinal image covers a sufficient number of sensitive retinal elements, so that consciousness receives a number of impressions separated from one another, sufficient to characterize the form of the object. It has been found that two points of an image must be at least $0·002^{mm}$ distant from one another when falling upon the *fovea centralis* of the retina, in order to give rise to two separate impressions. In other parts of the retina the distance must be even greater. For these reasons neither very minute nor very distant objects can be perceived by the eye.

The size (diameter) of the retinal image is evidently always determined by the size of the *visual angle*, which the two external lines of direction proceeding from an object form with one another: we therefore usually say that objects are not recognisable under a very small visual angle. In order to be able to recognise such objects the visual angle must be artificially increased, and with this object we employ in the case of small objects magnifying glasses and microscopes, in the case of distant objects, telescopes.

The magnifying glass is a convex lens; the object is placed within its focal distance, and therefore furnishes a virtual, erect and magnified image of itself (p. 369).

In the solar microscope the object lies outside the focal distance, near to the focal point, and furnishes therefore a real, magnified, inverted image, which is received on a screen. In the compound microscope the real image, which is similarly obtained, is not seen, but by means of a convex (collecting) lens it is brought somewhat nearer and diminished in size, and then is observed by means of a magnifying glass (eyepiece lens); it therefore remains inverted. In all dioptric telescopes a real, inverted image of distant objects is thrown by the convex lens of the object-glass. In astronomical telescopes this image is observed with the aid of a convex eyepiece lens, and it remains inverted and becomes virtual. In terrestrial telescopes, the real inverted image is looked at through a compound microscope which forms the object glass, and is therefore again reversed, and therefore seen erect; in the Dutch telescope (opera-glasses) the real image thrown by the objective becomes by means of an interposed concave lens (the eyepiece) reversed and virtual, and therefore the object appears erect.

By the magnifying power of optical instruments we understand the increase in the visual angle which is brought about by them.

In the case of instruments which furnish real images, as the solar microscope, the magnifying power is found simply

$$v = \frac{a_2}{a_1} = \frac{f}{a_1 - f} \quad \ldots \ldots \ldots \ldots \quad (1)$$

In all instruments which furnish virtual images the focal distance of the eye of the observer exerts an influence, for the virtual image to be distinctly seen must lie at the distance at which the observer is accustomed to see near objects clearly. If the eye of the observer is placed immediately behind the magnifying glass or eyepiece lens respectively, for the latter $- a_2 = s$. The magnifying power v of an ordinary magnifying glass is therefore $= \frac{s}{a_1}$, or, as by (32)

$\frac{1}{a_1} - \frac{1}{s} = \frac{1}{f}$, it follows that

$$v = \frac{s + f}{f}; \quad \ldots \ldots \ldots \ldots \quad (2)$$

The magnifying power of such a lens is therefore relatively less for short-sighted people than for others.

In the compound microscope the object-glass by itself, when f_1 is the focal distance, as in the case of the solar microscope, has a magnifying power found by the following formula:

$$v_1 = \frac{f_1}{a_1 - f_1};$$

the eyepiece, of which let the focal distance be f_2, magnifies by itself according to the following formula, $v_2 = \frac{s + f_2}{f_2}$.

The total magnifying power of the combination is therefore

$$v = v_1 \, v_2 = \frac{f_1 \, (s + f_2)}{f_2 \, (a_1 - f_1)} \quad \ldots \ldots \ldots \ldots \quad (3)$$

The distance between the object-glass and the eyepiece, *i.e.* the length of the microscope, must then be equal to the sum of the distances of the images of the object-glass, and the focal distance of the eyepiece required is therefore $-a_2 = s$; both the quantities to be added are found by equation (32), so that

$$\mathrm{L} = \frac{a_1 f_1}{a_1 - f_1} + \frac{s f_2}{s + f_2} \quad \ldots \ldots \ldots \ldots \quad (4)$$

Generally in microscopes L is given as unchangeable, so that a_1, the distance of the object from the object-glass, must be changed for every visual distance s; the magnifying power is obtained by eliminating a_1 from (3) and (4).[1]

Even the influence of the collecting lens can easily be calculated, though its introduction here would lead us too far.

In the case of astronomical telescopes the magnifying power is

$$\mathrm{v} = \frac{f_1 \, (s + f_2) \, a_1}{f_2 \, (a_1 - f_1) \, s} \quad \ldots \ldots \ldots \ldots \quad (5)$$

The length has the same value as in 4; as in this case a_1 is given by nature L must be changeable; from (4) it follows that the telescope must be drawn out the more, the smaller the magnitude of a_1, and the larger that of s. From (5) $\mathrm{v} = \frac{f_1}{f_2}$ and from (4), $\mathrm{L} = f_1 + f_2$; the length is therefore the sum of the focal distances of the objective and eyepiece. In opera-glasses it is, as can easily be seen, nearly equal to the difference of the focal distances.

The smallest distance at which two points in a retinal image can be separately seen is found by the following, amongst other, methods (Volkmann).

1. Two fine threads or lines, which are at a constant distance from the eye are approximated to one another until they can no longer be distinguished one from the other, and then the distance between their images on the retina is calculated. Instead of approximating the objects to one another, they can also be looked at with the aid of an apparatus for diminishing the size of objects (macroscope).

2. A point very near to the centre of suspension of an oscillating pendulum is looked at from different distances, until its movement is no longer perceptible. In these experiments *irradiation* must be guarded against. In the older determinations the smallest appreciable distance on the retina was found to correspond with the then accepted diameter of the cones (0.004^{mm}). New determinations have led to both the magnitudes being diminished, and even now an agreement between the two may be affirmed to exist.

The cones of the *fovea centralis* have a diameter of about 0.002^{mm}, but it appears that one ought to consider only the surface which bounds the outer and inner segment, which has a diameter of 0.001^{mm} (M. Schultze). As these surfaces naturally are at some distance one from the other, it may

[1] As the magnifying power of a microscope differs for different eyes, opticians base their statements as to magnifying power upon a conventional value of s (generally making it $0^{m}.25$).

possibly occur that in central sight minute points, as stars, form images which fall in the space between the cones, and so disappear. This actually does occur (Hensen).

For the perception of small images the mode of disposition of the mosaic of retinal elements is not without importance; in the yellow spot it is in the rhombic figures formed by the intersecting of neighbouring circles that the cones are situated.

The details of an image are distinguished partly by the difference in brightness, partly by the difference in colour. In the latter case the delicacy of the power of perception does not depend upon the number of the retinal elements, but upon the number of the elements capable of appreciating colour which are covered by the image. In the centre of the field of vision the two circumstances co-exist, as in this situation cones only exist; towards the periphery, however, the power of distinguishing colours diminishes far more rapidly than the power of discriminating differences in luminous intensity.

Subjective Images and Optical Illusions.

As nervous arrangements play a part in the perception of light, as of all other sensations, all the peculiarities of nervous excitability must be noted in connection with them; for example, *lesions* and *illusions*.

The same vibration of the ether will, for instance, give rise to a strong or weak impression, according to the degree of excitability of the end-organs of the optic nerve, or of its fibres, or even of the central organs connected with them. Other circumstances lead to actual errors, to a perception of a luminous impression independent of rays of light, or to the perception of other rays than those which are actually present (colour-illusions). Such impressions we call 'subjective.' The most frequent are the following:

1. *Persistent or after-Images.*—A fibre of the optic nerve having been excited, persists in its excited condition for some time after the exciting luminous ray has ceased to act, and the continuance is long and intense in proportion as the primary excitation was long and intense. In consequence of this, after every luminous impression, the object which has been seen remains visible for a very short time—an *after-image* being seen. Upon the property which has been alluded to depends the appearance of a fiery circle, which is seen when a burning coal is swung in a circular path before the eyes. The following instruments are based upon the existence of persistent images. The Thaumatrope is a disk rotating in front of the eyes, near the circumference of which a body which is continually moving is represented in the different successive stages of its movement, so that each figure can be perceived for a moment; each impression then persists until the following one succeeds it, and in this way the movement appears continuous.

The *coloured rotatory disk* (Newton's disk) is a disk turning with rapidity and divided into sectors of various colours ; the colour of one sector persists during one whole rotation, so that a mixture of many colours is presented to consciousness. If the original luminous impression is strong, the persistent (or secondary) image is at times dark, *i.e.* the excitability of the fibres has been for the moment diminished by fatigue, so that a dark place, having the same situation as the bright object seen at first, appears ; this is called *a negative persistent image.* At times positive and negative secondary images alternate for a period, *i.e.* the momentarily abolished irritability returns for an instant, so that the (positive) secondary image appears, to disappear again, &c. The secondary images offer some peculiarities when the primary impression has been due to an intense light or to a prolonged luminous impression. These images do not then appear of the same positive colour, but often of another *contrasting* colour, and often pass from one to the other successively. The contrasting colour is always that one which, if added to the primary colour, would give the tint of ordinary daylight (which is not pure white, but a little red), and therefore the ' contrasting' is very nearly the same as the ' complementary ' colour (Brücke).

Even white light appears after a luminous impression, amongst the ' contrasting colours ; ' if, for instance, we place a coloured piece of paper on a white surface, and stare fixedly at it for some time, and then look at the white surface, there appears a secondary image possessing the form of the coloured piece, but of the contrasting colour. The phenomena of contrast may be explained by supposing the exhaustion of the retinal elements which correspond to the primary colours.

Secondary coloured images appear also after impressions produced by white light, when these have been very intense (after looking, for example, at the sun); ordinarily a succession of divers colours appears, sometimes positive and negative colours alternating. This phenomenon of successive contrast of colours is probably explained by the excitation of the individual colour-perceiving elements lasting for different periods of time after the luminous impression has acted. In the peripheral parts of the retina these *contrast-phenomena* are modified by the red-blindness (and green-blindness), which are characteristic of these regions (Adamük and Woinow).

2. *Irradiation* becomes perceptible when a bright object on a dark ground is looked at ; the object then appears to be larger than it really is— conversely, a dark object on a bright ground appears smaller. This phenomenon results from defective accommodation, whereby the bright objects furnish blurred images.

Consciousness, under these circumstances, is inclined to add to the predominating part of the image the half-illuminated fringe (which is equal in width to the radius of the diffusion-circle) ; now, on the one side brightness predominates over shade, and on the other the object over the ground beneath it. If the ground is black, and the object white, the latter appears larger at the cost of the former; if, on the other hand, the object be black and the ground white, the second influence can preponderate so much over the first, that even black lines appear broader at the expense of the white ground (Volkmann).

3. *Simultaneous contrast* includes a series of phenomena which depend upon the comparison of two colours or tints bounding one another in the field of vision, as well as the illusion which results therefrom.

A white field appears the brighter, the darker its immediate surroundings (a white trellis-work upon a dark ground exhibits at the points of intersection apparently dark spots, for here the surroundings of the white spots contain less black than the remaining parts of the trellis); similarly, a colour appears the more intense, the more completely are its surroundings destitute of it, *i.e.* the nearer the surrounding medium approaches a *contrasting colour*. Conversely on a (feebly illuminated) white surface those components of white come out most strongly which are wanting in the vicinity; white thus appears in the contrasting colour of the vicinity (the shadow of a rod illuminated by a candle appears in daylight not white or grey, but is of the contrasting colour to the yellow candlelight, viz. blue).

The many examples of actions of simultaneous contrast which occur cannot here be referred to. Phenomena of contrast do not appear upon wholly unexcited places of the retina, so that the so-called *associated-sensations* are in no way identical with them (Rollett).

4. Amongst subjective phenomena are further to be mentioned the illusions as to colour which originate through the peripheral colour-blindness and the unequal excitability of the organs engaged in the perception of colours, *e.g.* very rapidly intermitting white light, as the luminous impression does not last long enough to excite the retinal elements which are sensitive to red, appears greenish (Brücke).

5. Excitations of the light-perceiving retinal elements due to causes which are purely internal, without external influence. To this class belong: *a.* Mechanical irritation, brought about by the circulation, and which only occurs where there is morbid irritability; under these circumstances appearances of sparks, lightning, &c. may be seen; sometimes there appears, especially before sleep, a complete image of the retinal vessels, with their contained blood-corpuscles, &c. *b.* Central excitations of unknown origin and manifesting themselves in the most diverse forms ('hallucinations,' 'phantasms'); these are seen especially in dreams, in the half-waking state, before going to sleep, and in diseased conditions even during the waking state.

Entoptical Perceptions.

'Entoptical' phenomena are to be clearly distinguished from such as are subjective. Entoptical phenomena are visual impressions of objects which are present within the eye itself. The most important of such phenomena are: 1. Perceptions of opacities and obscurations of the refracting media of the eye. These are apparent when, by illuminating the eye, their shadows fall upon the retina, and they are best seen when parallel luminous rays traverse the eye.

They appear in the form of dark spots, balls, streaks, rows of pearls, &c.; in part, they are fixed, in part (those of the vitreous humour), they change their position, especially during sudden movements of the eye or of the head.

2. Perceptions of the retinal vessels, brought about by their shadows falling upon the layer of rods. In order to bring out these shadows they are directed upon the lateral parts of the retina, which are seldom lighted up, by causing an intense light to fall upon the transparent sclerotic, or the shadows are made to move by causing a luminous point to pass backwards and forwards before the eye. Under these circumstances a dark delineation of the vessels, on an illuminated field, is perceived; even the border of the *fovea centralis* is recognisable by a shadow (Purkinje's figures).

3. The perception of the blood-corpuscles in the retinal capillaries, when the eye is very feebly illuminated (as by a layer of snow, a lamp-globe, or (Grünhagen) a dark blue glass held before the sun); this phenomenon is, as yet, not fully explicable.

Movements of the Eye.

The eye is capable of very extensive movements in the orbit, and the absolute mobility of the organ of vision is considerably increased by that of the head as a whole. Hence it is possible in any position of the body to observe objects in all situations of space, *i.e.* so to place the eye as to cause the retinal image of any object to fall on the *fovea centralis retinæ*. The great mobility of the eyeball depends upon the mode of its attachment to the orbit. It rests on the pad of fat of the orbit, as the head of a bone in a ball and socket joint rests in the hollow cavity, and it can therefore rotate around innumerable axes. These movements, which are effected by the muscles of the eye, are held in check, firstly, by the points of attachment of antagonizing muscles, and, secondly, by the attachment of the optic nerve. In addition to the movements of rotation, changes in the position of the globe as a whole can occur in consequence of the yielding nature of the surroundings—in this case ' the joint-cavity is displaceable' (Ludwig).

The point of rotation of the eyeball (in the sense referred to at p. 291) does not lie, as was surmised *à priori* and as was concluded from researches (Volkmann), in the middle of the visual axis, but (Donders and Doijer, Fick and Müller) in the case of normal eyes 1.77^{mm} behind it.

It is to be noticed that when the eyelids are forcibly opened, the eyeball protrudes somewhat from the orbit, probably by the contraction of both the oblique muscles; the movement forwards is most marked when the eyes look horizon-

tally or downwards, and then it amounts to about 1^{mm} (Fick and Müller).

· To understand the changes in the situation of the globe and the arrangement and mode of action of its muscles, we must assume the existence of certain fixed points and lines in the eyeball, the changes in the situation of which furnish a measure of the movements of the eye. One line in the eye is given by its anatomical construction, viz. the *visual axis*, which is the *principal ray* proceeding from a fixed point, the situation of which in relation to the axis of the cornea has already been referred to (p. 397). Starting from the *fovea centralis,* which may be considered to be one pole of the eyeball, two meridians at right angles to one another may be drawn on the retina. Their position is determined by certain physiological properties of the eye ; they divide the retina into four quadrants which have in the two eyes certain reciprocal relations, and they are called *lines of separation* (one of which is horizontal, the other vertical).

If we now imagine a plane passing through the eye at the centre of the visual axis and perpendicular to it, it will cut the spherical surface in a great circle perpendicular to the meridians, which we designate the *equator* of the eye, the plane being termed the '*equatorial plane.*' We have then three great circles perpendicular to one another (the equator and two meridians); the planes corresponding to these circles intersect one another in three diameters at right angles to one another ; these are : one sagittal (the visual axis); another vertical, and a third horizontal. These may be employed as a system of co-ordinates movable with the eye and indicating its movements. A second system of co-ordinates absolutely fixed in space, and coinciding with the movable system when the eye is in its position of rest, must also be assumed to exist. In any other position of the eye two or three of the corresponding axes of the two systems must form angles with one another.

The movements of the eye are especially of importance in bringing about the combined positions of the eyes and are limited by the latter. That position is assumed as the *position of rest,* from which all movements may be supposed to start. This so-called '*primary position*' is one in which all three axes of one eye are parallel to those of the other, and the transverse

axes lie in one straight line, the visual axes being therefore antero-posterior (sagittal) from within outwards.

It is obvious that this position can be associated with a voluntary *inclination* of the visual axes to the horizon. Amongst all such possible positions there is one to be mentioned as a *primary position*, properly so called, namely, that inclination in which convergent movements of the visual axes may occur without the eyes requiring visibly to rotate around their visual axes, as is the case in all other positions. The determination of this inclination will be given below. It has now been established (Listing, Meissner, Helmholtz) *that when the eye moves from the primary position, its movements take place around axes situated in the equatorial plane (so that the visual axis is always perpendicular to the axes of rotation and that rotations never take place around the visual axis).* Amongst the innumerable axes which may be supposed to exist in the equatorial plane, there are two which are first to be mentioned, viz. those which are at the same time co-ordinate axes, viz. the transverse axis and the vertical axis. Rotations around these two axes lead to the ' *secondary positions* ' of the eye. Rotation around the first merely occasions an alteration of the inclination towards the horizon and the parallelism of the axes continues; rotation around the vertical axes produces a rotation inwards or outwards, and consequently a convergence or divergence of the visual axes, the inclination to the horizon continuing the same. Thus in the first case the plane of vertical separation, but not that of horizontal separation, coincides with that which corresponds to it in the fixed system of co-ordinates; in the second case the converse is true.

Rotations around other axes lying in the equatorial plane of the eyeball lead to ' tertiary positions ' of the eye. As every such rotation can resolve itself, according to simple rules, into a rotation around the vertical axis and a movement around the transverse axis, it follows, in the first place, that tertiary positions are as much associated with convergence of the visual axes as with their change of inclination to the horizon, and, secondly, that neither the vertical nor the horizontal plane of separation coincide with the planes which correspond to them in the fixed system of co-ordinates; they are both inclined the one to the other. The eyes have therefore undergone in the tertiary posi-

tions *an apparent rotation around their visual axes*, in the same direction as the hand of a watch moves, when directed to the left looking upwards, when to the right downwards. Every position of the visual axes is therefore associated with a certain rotation of the eye, which can be deduced from Listing's law.

If a be the vertical and β the horizontal deviations of the visual axis from the primary position, the angle of rotation ('Raddrehungswinkel') is found by the equation (Helmholtz)

$$- \operatorname{tang} \gamma = \frac{\sin a \sin \beta}{\cos a + \cos \beta},$$

or

$$- \operatorname{tang} \frac{\gamma}{2} = \operatorname{tang} \frac{a}{2} \operatorname{tang} \frac{\beta}{2};$$

these equations show that when $a = 0$ or $\beta = 0$ (secondary positions) the rotation is 0.

If we denominate the plane of both visual axes the *visual plane*, then the horizontal meridian of the retina, either in the primary or secondary position, coincides with the visual plane, but differs from it in tertiary positions; the angle which both planes form is the *angle of circular rotation*. With the help of the visual plane the positions of the eye can also be defined as follows. In the primary position the visual plane has a determined inclination; the visual axes are parallel and perpendicular to the line which unites the points of rotation of the two eyes. Secondary positions arise either when the visual plane alters its inclination, the visual axes remaining fixed in it, or when the visual plane remaining fixed, the visual axes change their position in it. All other positions are *tertiary positions*.

The necessary result of Listing's law, according to which every deviation of the visual axes from the primary position indicates the inclination of the meridian of the retina to the visual plane, and therefore the position of the whole eye, can be deduced from the 'principle of the easiest orientation' (Helmholtz). As, namely, the orientation in vision depends upon the appreciation by our consciousness of the position of the visual axes in reference to the head, and upon our estimation of the 'angle of rotation,' we need not calculate the latter. We learn by experience, or probably by an inherited automatism which had its origin in experience (refer to the review of Darwin's principle in Chap. XII.), to associate with every position of the visual axes a definite 'angle of rotation.'

A further mathematical extension of the 'principle of easiest orientation' teaches that the most convenient point of departure (primary position) is that in which the visual axis is exactly in the centre of its field of movement (*i.e.* in the centre of the cone of the orbit, and that it can only deviate from this position by rotations of the bulb around the diameter of the equatorial plane (Listing's law). The primary position is in fact the *median position* of the eye.

The newly discovered facts (Javal, Skrebitzky, Nagel) that when the head is inclined to either side a true (compensating) circular rotation takes

place, which appears to be immutably connected with the movement of the head, in no way contradicts Listing's principle.

Let Fig. 24 represent a vertical plane placed before the eye at the (reduced) distance A B, and let *p* be its point of intersection with the visual axis in the primary position. If the eye now looks at any other point of intersection of the figure, the lines (correspondingly reduced) represent the direction in which the planes of the horizontal and vertical meridians of the eyeball intersect the observed plane. It can be seen that these directions remain horizontal or vertical in secondary positions, *i.e.* in positions within the lines *h h* and *v v*; in all other (tertiary) positions, however, the circular rotation must deviate from the horizontal or vertical direction. If in the primary position the vertical strongly-marked cross at *p* be looked at fixedly, so that a *persis-*
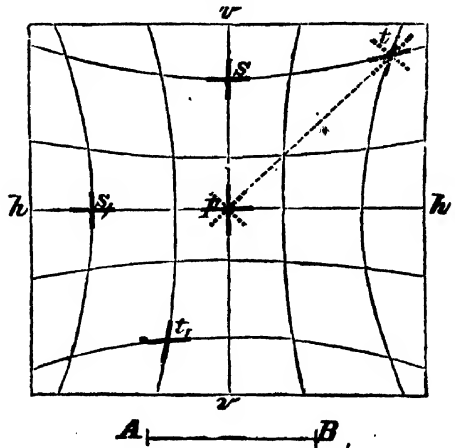
Fig. 24.

tent image is impressed upon the vertical and horizontal meridians, that image remains unaltered in the secondary positions (*s*, *s₁*), but takes up in the tertiary positions *t* and *t₁* the situations given, appearing therefore oblique, and at the same time no longer rectangular, corresponding to the lines of intersection of the two meridian planes with the observed plane. If the cross at *p* were placed like the dotted cross, so that one of its limbs fell on the line *p t*, no distortion of the secondary image occurs at *t*. If the plane which is looked at be provided with horizontal and vertical lines, Listing's law may easily be proved and confirmed by means of the situation of the secondary images (Helmholtz).

The Muscles of the Eye.

The mode of action of each individual muscle of the eye, *i.e.* the position of the axis, around which, if it acted independently, it would move the eye, can be calculated, provided that the situation of its origin in the orbit and the position of its attachment to the bulb be known. The situation of these points is expressed by the length of the abscissæ cut off by the perpendiculars drawn from them to the three fixed co-ordinate axes.

The situation of the axis is determined by the three angles which it forms with the three co-ordinate axes of the eye in its initial position. In this way the following positions of the axes have been determined in the case of the six muscles of the eye

(Fick); the initial position coincided approximately with the primary position.

Muscles	Angle which the axis of rotation forms with the		
	Visual axis	Vertical axis	Horizontal axis
Rectus superior	111° 21′	108° 22′	151° 10′
„ inferior	63° 37′	114° 28′	37° 49′
„ externus	96° 15′	9° 15′	95° 27′
„ internus	85° 1′	173° 13′	94° 28′
Obliquus superior	150° 16′	90° 0′	60° 16′
„ inferior	29° 44′	90° 0′	119° 44′

For the chosen initial position there does not exist, as may be seen, any axis of rotation in the equatorial plane of the eye, otherwise it would form a right angle with the visual axis. The axes of rotation of the internal and external recti are very close to the vertical axis, so that actually they rotate the cornea almost simply inwards or outwards. The axes of the two oblique muscles, on the contrary, are situated exactly in the horizontal plane, at each side of the visual axis, each being at a distance of about 30° from it, so that the rectus superior draws the cornea outwards and downwards, whilst the rectus inferior draws it outwards and upwards. The axes of rotation of the recti, superior and inferior, are considerably deviated from the horizontal axis, so that the former rotates the cornea upwards and inwards, the latter downwards and inwards. From the angles we conclude that each of the three pairs of muscles has approximately a single axis, and therefore acts almost antagonistically to the others.

As all the real movements of rotation of the eye are effected around the diameter of the equatorial plane, it follows that several muscles must co-operate in the production of almost any movement. This has actually been ascertained to be the case with eyes which have been partially paralysed.

Fig. 25 exhibits a horizontal section of the left eye; ss_1 is the visual axis, and qq_1 the transverse axis. This plane contains, according to what was previously stated, the axes of rotation of the recti rr_1 and of the oblique muscles oo_1.

If the moments of rotation be expressed by lines corresponding to the axes of rotation, and drawn to the one side or to the other of the point of rotation, these moments of rotation

may, in a manner quite analogous to the parallelogram of forces, be combined into resultant moments of direction; the diagonal of the parallelogram gives by its direction the situation of the resulting axis of rotation, and the direction of the rotation, whilst its length furnishes the magnitude of the resulting rotating force. Conversely, rotations can be decomposed according to given axes. Thus the diagram shows that to produce a rotation of the bulb around the horizontal axis to the extent $c\,q$, the rectus superior and obliquus inferior

Fig. 25.

must act together, and in the relations indicated by $c\,a$ and $c\,b$. For an equal rotation $c\,q$, in the opposite direction, the obliquus superior and the rectus inferior must co-operate in the relations indicated by the lines $c\,d$ and $c\,e$.
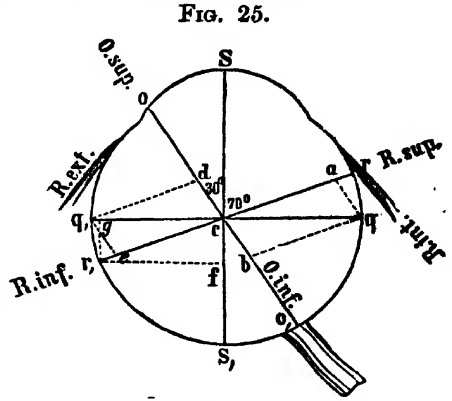
Further, the figure shows that the rectus inferior by itself can bring about not merely a rotation around the horizontal axis $c\,g$, but also one around the visual axis ($c\,f$). The consideration and estimation of muscular action necessary to produce any given movement are such very complex processes, especially because as soon as the smallest changes in the position of a muscle have set in its axis of rotation has become altered, that the subject cannot here be pursued further.

The nerves which preside over the movements of the eyeball are, the oculomotor (3rd), the N. abducens (6th), and the trochlear nerve (4th). These nerves, which contain a large number of fibres, and the actions of which can be varied with great rapidity, are united on the two sides of the brain by a certain bond, which tends to limit the movements brought about under their influence. This association leads, in the first place, to only such movements happening, as result in both visual axes being in the same plane (visual plane), so that when they are not parallel, if prolonged, they meet and intersect at a point; they have, therefore, so long as the head is held erect, the same inclination towards the horizon, for the two points of rotation can be considered fixed. Further, their reciprocal inclination is limited, so that they only diverge to a very slight extent

anteriorly, whilst they can converge to any required extent in so far as their position will admit of it. The mechanism by which this association of movements is effected is altogether a puzzle. Deviations from its normal condition constitute squinting (strabismus). The central organ, which co-ordinates the movements of the eye, is situated in the corpora quadrigemina.

Binocular Vision.

Normally the two eyes act together, and the advantages which result from this association are the following: 1. Correction of the faults of the one eye by the other. 2. The perception of space is more perfect, because when we look at an object from two different points of view, instead of observing a mere projection of it in a surface, its third dimension in space is appreciated. 3. A more accurate estimate of the magnitude and the relative distances of objects is formed.

Simple Vision.

Though we look at external objects with both eyes, these in general are seen as single; this can only depend upon the fact that the excitation of certain associated spots on the two retinæ is referred by consciousness to the same point in space—or, in other words, that both eyes possess but a single, common, field of vision, and that the luminous impression which originates by the excitation of two associated points, appears at one point in the field of vision. Such associated points are called *corresponding* or *identical* points. An object which is seen single by the two eyes, whatever their position, must therefore project its image on the two retinæ in such a manner that the two points of the image which correspond to one point of the object fall upon corresponding points on the retinæ. If one of the two eyes be deviated, to however small an extent, a double image must at once originate. We shall subsequently refer more in detail to the nature of ' Identity.'

Situation of Corresponding or Identical Points.

Concerning the relative positions of corresponding points, the following laws are apparent :

1. As an object c, which is looked at fixedly by both eyes, and the images of which fall, consequently, upon the terminations of the visual lines c and c_1, is seen single, the two terminations of the visual axes c and c_1 must be corresponding points.

2. If the centre, c, of an object, which is seen single, be looked at, it follows, as the simple construction of the figure shows, that the identical points which correspond to all points
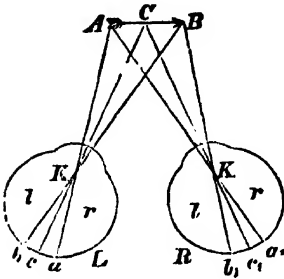
FIG. 26.   FIG. 27.
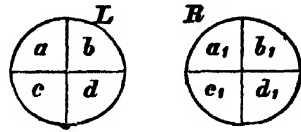
of the right half of the retina, lie on the right side of the other retina also, and conversely. Further, that the upper half of the retina of one eye corresponds to the upper half of the retina of the other eye, and the lower half of the one to the lower half of the other.

Let the circles L and R represent projections of the two retinæ, the similarly designated quadrants a, a_1, &c., are corresponding. The two meridians which separate these identical quadrants are called lines of separation (vertical and horizontal)

3. It follows, further, that corresponding points on the two vertical lines of separation must be identical, and this is also true of points on the horizontal lines.

If in a given position of the eye the visual rays belonging to two corresponding points be drawn and prolonged beyond the eye until they intersect, the points of intersection will evidently be the points which in that position of the eyes appear single. The term *horopter* is given to the combination of all those points in space which, for any one position of the eyes, appear single. If the horopter had been perfectly determined for any position of the eyes, the relation in the position of corresponding points would obviously be likewise determined, and the horopter for any other position of the eyes might be constructed. Conversely, when the relation of the situation of

these points is known, the horopter for any position of the eye can be deduced. In so far as the relative positions of the points, the most simple statement is the following : *If the two retinæ, with their corresponding lines of separation, be imagined to be superposed, all the points which coincide, or touch, are corresponding points.*

This statement is not rigorously true, even if the form of the retina, which is not perfectly spherical, be taken into account. The vertical meridians are not perfectly identical, and the true vertical lines of separation do not exactly coincide with them, above being inclined outwards, and below being inclined inwards. The physiological vertical axis is therefore somewhat inclined to the geometrical axis.

With the help of the above data the horopter can be determined mathematically or geometrically. The results of calculations are confirmed by experiments, and the latter establish the correctness of the relations in the position of corresponding points on the retinæ.

A general deduction relating to the horopter can be arrived at by the following method (Helmholtz). Every point on the retina may be considered as a point of intersection of a meridian and of a ' parallel circle ' (parallel circles being such concentric circles as pass around the *fovea centralis*, which is the pole of the retinal sphere). It is possible to calculate, 1, the ' meridian horopter,' *i.e.* the assemblage of lines of intersection of two planes passing through identical meridians and the nodal points ; 2, the ' circular horopter,' that is to say, the assemblage of the intersections of two conical surfaces passing through identical parallel circles and the nodal points ; 3, the point-horopter, *i.e.* the horopter of corresponding points, which obviously is the intersection of the meridian and circular horopters.

A second method of deduction (Hering, Helmholtz) considers the plane of the vertical meridian as rotating around the vertical axis, and the plane of the horizontal as rotating round the horizontal axis ; the sections of retina so obtained are termed longitudinal and transverse sections. Longitudinal sections which make the same angle with the plane of the vertical meridian are identical. The lines of intersection of the planes of corresponding longitudinal sections constitute together the ' horopter of the longitudinal sections.' Similarly, the identical transverse sections form a system of intersecting lines—the

horòpter of the transverse section. The intersection of the two horopters is the point-horopter sought for.

Both methods must, if rightly carried out, furnish the same results. Each method possesses special interest, for not only the point-horopter, but the line-horopter is of importance. This remark specially applies to the previously mentioned meridian horopter. A straight line, which is fixed at one point, naturally forms an image of itself in a meridian of the retina. If now a line throws an image upon two identical meridians, it must appear single, even though its individual points do not fall upon identical points, for the double images then are superposed in the field of vision, as the lines A B and $a\,b$ in Figure 28. The meridian horopter or the normal surface

Fig. 28.

| A | a | B | b |
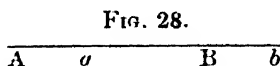
(v. Recklinghausen) possesses the property that all straight lines falling upon it appear single, though all the points lying in it do not do so.

For practical purposes the second of the two methods previously referred to is more convenient, chiefly because it permits of our taking into account the deviation of the physiological vertical meridian. The results of the calculation cannot here be discussed, as an exhaustive treatment of the difficult problem of horopters would not be consistent with the object of this handbook, and instead of attempting it, those determinations of horopters will be treated of which can be arrived at by simple geometrical considerations.

1. *In the primary position, and in secondary positions when the visual axes are parallel and directed forwards*, the horopter is a plane parallel to the plane of vision passing through the point of intersection of the vertical axes of the two eyes. As it is the physiological vertical axes, however, which are here concerned, and as their point of intersection is situated about five feet below the field of vision, it follows that the plane of the horopter, which would otherwise be at an infinite distance below, is only five feet below the visual plane. If therefore we look horizontally into infinite distance, the ground constitutes the horopter-surface—a fact which is of great importance for sight in this position (Helmholtz).

2. *In secondary symmetrical positions, when the visual axes are convergent,* the horopter is as follows : two lines in the horopter must be determined, viz. one which corresponds to the identical points in the horizontal lines of separation, and one which corresponds to the identical points in the vertical lines of separation (a transverse section of the horopter formed by the plane of vision, and a median section of the horopter).

(*a.*) *The transverse section of the horopter* is a circle (J. Müller). In Fig. 29 the two transverse sections of the eyes pass through the horizontal lines of separation. The transverse section of the horopter must therefore be in the plane of the paper (visual plane) ; *c* and *c₁* are the extremities of the visual axes, c is the fixed point. If now for two points, as *a* and *b* in the horizontal line of separation, we seek the identical points on the other side, the latter must evidently, 1, lie on the same side of the termination of the visual axis ; 2, be equally distant from the visual axis ; they lie therefore at a_1 and b_1. The

Fig. 29.
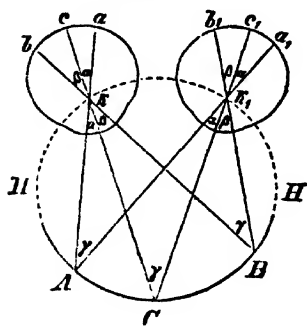
visual rays which belong to these intersect at the points A and B, which are therefore points in the horopteric line sought for. It is readily seen by looking at the drawing of the angles at the nodal points k and k_1 that the angles at A, B, and C (γ) are equal. As they all proceed from the common points k and k_1, they must be all peripheral angles of a circle H H, passing at once through k and k_1. But as this is the transverse horopter-line sought for the visual rays proceeding from all the other identical points on the lines of horizontal separation must here intersect.

(*b.*) The median section of the horopter, on the other hand, is a straight line, perpendicular to the visual plane, and therefore inclined to the horizon—the line in which the two planes which pass through the vertical lines of separation intersect. This is most easily understood if Fig. 30 be drawn upon a piece of paper, which is then cut through along the line H H, so that the two sides can be made to converge. The two sections of the eye pass through the vertical lines of separation in such a manner that the two converging planes which cut at H H are the planes of the vertical meridians. It can be seen

at a glance that the visual rays of all the points in the lines of separation which are equally distant from the terminal points c and c_1 of the visual axis, e.g. a and a_1, b and b_1 meet in points on the intersecting line H H, and that the latter therefore represents the median horopteric line. This horopter for the converging secondary positions is limited by the two lines just alluded to.

3. In (symmetrical) tertiary positions the vertical lines of separation, as well as the horizontal lines of the two eyes, meet
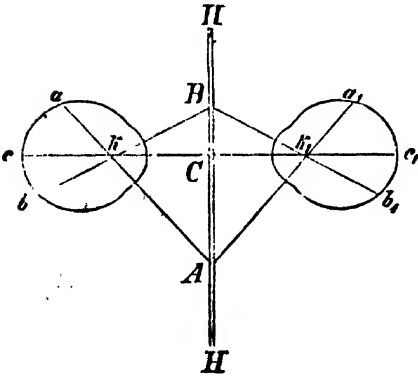
Fig. 30.　　　　　　　　　　Fig. 31.
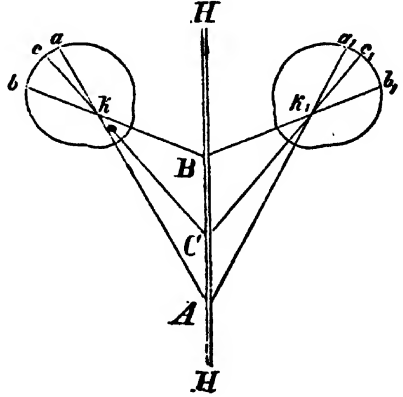
at an angle. If now (a) a plane is made to pass through each vertical line of separation, the two planes intersect in a straight line, which is inclined to the visual plane (nearer to the eyes superiorly in tertiary positions, with these eyes inclined upwards, nearer to the eyes inferiorly in tertiary positions in which the eyes are directed downwards). This inclined line, as well as the inclined position of the vertical lines of separation, are rendered evident by the annexed Figure 31, which like 30 should be drawn upon a piece of paper, and be split up along H H. In the model c c c_1 is the visual plane, and H H is the line of intersection of the two planes of separation, and which is inclined as in Fig. 30. It is seen that the visual rays of all the corresponding points situated in the vertical lines of separation, for example a and a_1, b and b_1, intersect also in the line H H, and that this line represents in consequence the horopter of the vertical lines of separation.

(*b*.) If planes are made to pass through the horizontal lines of separation, these likewise cut in a line. The visual

rays of identical points of the horizontal lines of separation, if they do intersect, could therefore only do so in this line. But if from any point in the latter two visual rays be drawn, these rays meet, as can readily be seen, in *symmetrical but not in identical* quadrants of the vertical circles of separation. Hence it follows that the visual rays proceeding from identical points of horizontal lines of separation do not in general intersect, in tertiary positions, and that for these there is consequently no horopter. In general, the horopter for tertiary positions, besides the meridian line, only includes another curve of double curvature passing through the fixed point, and which cannot be here considered.

Hitherto only symmetrical positions of the eyes have been discussed. It is impossible here to examine in detail the unsymmetrical positions in which the fixed point is at unequal distances from the nodal points. It is to be remarked, that positions occur in which the fixed point alone forms the horopter.

In addition to the horopter of points which has hitherto been considered, the horopter of meridians or the normal surface, whose properties have already been referred to at p. 413, is to be mentioned.

This surface (v. Recklinghausen) in secondary convergent positions is a plane perpendicular to the visual plane in the fixed point ; it is in tertiary symmetrical positions a double oblique cone whose summit lies at the fixed point. From this first property this important consequence follows, that in every plane inclined before the eye, assuming that it be considered in a secondary position, as is ordinarily the case, *every straight line must appear simple, providing that one of its points strike the eye.* Experiments have, however, revealed that all the straight lines lying in the normal surface, and none but such lines, appear perpendicular to the meridian plane, even in tertiary positions, where their real direction is quite different. If, for example, we look at a star formed of threads, whose rays lie in one plane, and fix our eyes upon its middle point, it will appear plane only in secondary positions, and curved in tertiary positions, and its rays then are deviated from the plane surface apparently in a direction opposed to that of the normal surface ; the star only appears lying in a plane, in tertiary positions, providing an

artificial curvature corresponding to the normal surface be given to it.   Other researches show that every luminous point, whose distance cannot be determined by other methods, is projected in the line of direction into the normal surface.   This surface appears therefore to be familiar to our eyes, and very probably it plays a very important part in stereoscopic vision, for the position of every part which does not lie within it is determined in accordance with it.

In order to explain this relation of corresponding points, one might surmise that the fibres of the optic nerve which belong to them are connected in the central organ in a peculiar manner so that their excitation only occasions one single act of consciousness, or at least that the two impressions are transferred to one and the same place in space, viz. to the point of intersection of their visual rays.   Many interpret in this fashion the relation of the fibres of the optic nerve in the *chiasma nervorum opticorum.*   It is highly probable that in this situation a transfer of one half of the fibres from one side to the other occurs, so that each optic nerve-trunk is composed, half of fibres derived from the *optic tract* of one side, the other half being made up of fibres of the optic tract of the other side; each tract must furnish fibres to the two halves of the retina which possess the same name, and which therefore are *corresponding,* the halves being limited by the vertical lines of separation.   In support of this view, the occurrence of hemiopia, in which in both eyes the retinal sensibility of the same half of the retina has been lost, may be adduced.   In this case we must suppose that the fibres of, and the nerve centres connected with one of the optic tracts, are incapable of discharging their function (v. Graefe).   In opposition to this view a complete crossing of the fibres has lately again been stated to occur in the chiasma (Mandelstamm).   In this case hemiopia of both sides would not be caused by an affection of one tract, but by an affection of the outer angles between the tract and nerve, whilst an action upon the anterior angle of both nerves would lead to disturbance of the inner portions of the retina, and one affecting the posterior angle of both tracts would lead to disturbances in the outer portions of the retina; true hemiopia with exact demarcations in the vertical meridian yet would remain without explanation.

The correctness of the view that a central anatomical union of corresponding points exists is, however, still doubtful, because the 'identity' of such points is not to be taken in an absolute sense (compare below under Stereoscopy), but should perhaps be looked upon as a property acquired by habit. Further, in no case can the anatomical union of the corresponding points be such that the excitation of two points produces a single sensation, for the phenomena of stereoscopic vision, when the illumination is sudden, prove that stereoscopic vision depends upon the fusion of two separate sensations.

Non-Perception of Second Images.

It results from what has been previously stated, that in consequence of the limitation of the horopter in all positions of the eyes, the majority of objects before the eye appear double, and that, moreover, disorders and variations must be produced in the field of vision of the two eyes, because the rays proceeding from different points of the object fall upon identical points. If, in spite of this, we have in general only the consciousness of simple images, and fail to see any perturbations in the field of vision, it is because the following circumstances are probably in operation:

1. Objects which furnish images which fall on the centre of the retina (*fovea centralis* and *macula lutea*) appear simple under almost any circumstances, because the terminal points of the visual axes are corresponding points, and these axes, if prolonged, intersect at one point. Now as this is the seat of the most acute vision, and as the attention is almost constantly fixed upon it, the influence of the light falling upon it preponderates over the influence proceeding from the whole of the rest of the field of vision.

2. Objects which appear simple (which lie in the horopter) can impress consciousness with greatest intensity, seeing that they excite with double energy the same part of the nerve centres.

3. The eyes are always accommodated for those objects for which their axes are suited, so that they appear more sharply defined than those which are placed in front of or behind the point of intersection of the axes, and which are therefore not situated in the horopter.

This relation between the movements of the eyes and accommodation is brought about at first by the will, afterwards with the co-operation of a nervous mechanism (Czermak); in fact, the slightest movement of rotation of the eye is accompanied by a change in its accommodation, *e.g.* when the eye is rotated inwards it is accommodated for near objects.

4. Consciousness fuses, under certain circumstances, images of points which do not really correspond (see under Stereoscopy).

Co-operation of the two Eyes in Vision.

The most obvious advantage of vision with two eyes is, that portions of one retina which are incapable of discharging their function, *e.g.* by disease (v. Graefe), or portions of the retina which through opacities in the refracting media cannot receive images, are compensated for by corresponding points in the other retina. It is in consequence of this function of double vision that the mutual replacement of the gap in the field of vision due to the blind spot is filled up, for the corresponding points to the blind spots are parts of the retina which are sensitive to light (the blind spots are situated in retinal quadrants of different names, but symmetrical).

Stereoscopic Vision.

Stereoscopic vision, the perception of the third dimension occupied by bodies in space, depends upon the circumstance, that the two images of a material object or of a surface, which do not coincide with the horopter, can never be completely united (according to the theory of corresponding points) so as to furnish one single visual impression. As the two eyes contemplate the object from two separate points of view, two separate perspective images fall upon the two retinæ. Now only exactly corresponding retinal images can uniformly fall upon corresponding points; when the eyes remain immovable only one part of a body can therefore appear single, the rest appearing double.

If, *e.g.*, L and R (Fig. 32) are the two perspective retinal images of a truncated pyramid, the summit of which is directed towards the eyes which contemplate it, it is seen that either the images of the surfaces of the base, viz. $a\ b\ c\ d$ and $a_1\ b_1\ c_1\ d_1$, or the images of the truncated surface $e f g h$ and $e_1 f_1 g_1 h_1$,

can alone fall upon corresponding points of the retina; in the first case, the smaller (truncated) surface appears double, in the second, the larger. Nevertheless, the two images are fused into one, and convey the impression of a single body occupying

FIG. 32.
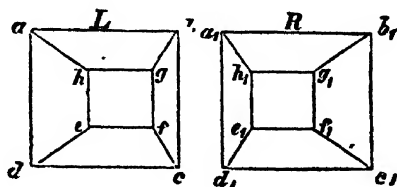
three dimensions. A simple explanation of this phenomenon would appear to be the following (Brücke): the two eyes are continually in a state of motion; their position of convergence varies so far from one side to the other, that, one after the other, the images of all sections of the pyramids fall upon corresponding points of the retinæ.

In Fig. 33, three of the fusion-impressions which occur in two series of movements have been selected for examination. In the first the images of the basal-surfaces, and in the third those of the truncated surface, fall upon corresponding points; the image of a section of the pyramid situated between the two first $(i\,k\,l\,n)$, and placed in the centre of the two first, is

FIG. 33.
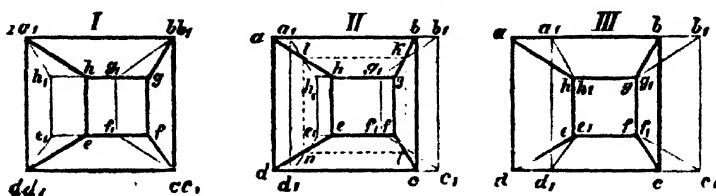
seen simply by the eyes. As now, in order that the impression exhibited by Fig. 33, III., shall be perceived, the eyes must converge more strongly than for the perception of I.; and as the convergence of the eyes affords a means of determining the distance of objects from them (see below), the conclusion is arrived at by consciousness, that the surfaces $e\,f\,g\,h,$ $i\,k\,l\,n,$ and $a\,b\,c\,d,$ lie one behind the other, and the conception of a material object is arrived at, through the combination of all the rapidly succeeding impressions.

But the fact that the exceedingly short space of time during

which an electric spark lasts suffices to fuse two simple stereoscopic images into one material impression, appears to afford an argument in opposition to the explanation above given, for in the moment of time during which the spark lasts no movements of the eyeball could take place.

This observation compels us to modify somewhat the theory of binocular vision. The identity of two corresponding retinal points is, namely, not to be taken as absolute, presumably does not depend upon a direct anatomical communication, but *is something which is acquired.*

Corresponding points are therefore such points as furnish images which, as experience teaches, are habitually combined or fused. But as it appears necessary to effect these combinations in order to obtain correct impressions of objects, we get into the habit of fusing also the images of two not perfectly corresponding points which under ordinary circumstances we should perceive as double. It can easily be demonstrated that simultaneous images, which fall upon corresponding points, are not united, although it is true that they do not form second images. When the mind must unite images which do not fall upon corresponding points, the process must be associated with the conception that the corresponding points in the object occupy the situation for which the eye would have to be arranged, in order that the images should coincide.

We cannot here enter into an examination of the numerous theories which have been advanced in explanation of the above-mentioned facts. Moreover, Brücke's explanation of the stereoscopic fusion is not entirely refuted by the experiment of instantaneous illumination which was previously adduced, as, for the vision of complicated objects, such a movement of the eye from side to side is, at any rate, very useful. For the vision of such objects momentary illumination does not suffice.

Stereoscopic vision can be artificially imitated by placing before each eye the drawing of a body executed from its own point of view; such drawings are shown in Fig. 32. The eyes in this case bring either successively or at the same moment the different parts of the drawing over corresponding points, and so the impression of the shape of body is produced. This is the basis of the stereoscope. Without further apparatus the images R and L, which lie side by side, may combine, if we direct each

of the two optic axes to the corresponding image (Fig. 35). But inasmuch as few persons can control their eyes for a suffi-

Fig. 34.

cient length of time, in order to fix two separate points on a surface, instead of allowing as usual the axes to intersect at the surface which is looked at, arrangements are provided whereby this exertion is dispensed with, so that with an ordinary position of the eyes, images are thrown upon corresponding points. The two best known stereoscopes are those of Wheatstone (Fig. 35) and Brewster (Fig. 36), which are explained by the annexed figures.
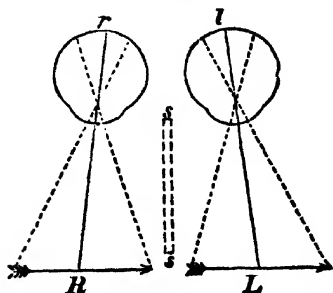
In the first (Wheatstone's) stereoscope the images are superposed by two converging mirrors, in the second (Brewster's) by two prismatic glasses $g\ g$ (halves of lenses) upon a place R, to which the optic axes are directed.

Fig. 35.
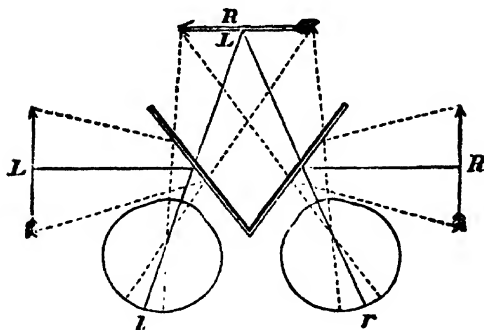
Fig. 36.
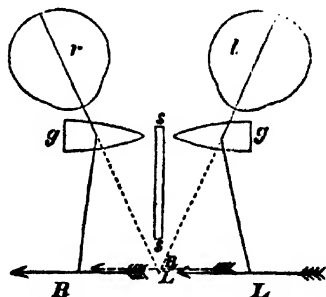
If two perfectly similar drawings are placed in the stereoscope, they naturally furnish a single image. If they are, however, ever so little different, the difference even being limited to the situation of certain parts, the eyes are compelled to make movements in order to combine these parts, and they appear, from what was previously stated, as removed from the surface, being either in front or behind it. Hence the stereoscope may be employed in order to distinguish between two similar objects which differ only in small and limited points, as, for example, between a real and a forged bank-note, as between two (different) impressions from the same mould, &c. (Dove).

If the relative positions of the stereoscopic image of a body

be changed, for example, those seen in Fig. 32, so that the one intended for the right eye is brought before the left, or conversely, the body appears hollow and as if seen from within, the smaller surface, $efgh$, appearing to be placed behind the larger. Actually the perspective views obtained by both eyes from a hollow pyramid, seen from the interior, only differ from those which are obtained on looking at a massive pyramid from the outside, in the fact that in the first case the right eye obtains the view which in the second case reaches the left eye.

On looking at an object from the outside, the right eye catches more of the right side of the object than of the left (the surface $b_1 c_1 f_1 g_1$ (Fig. 32) is therefore larger than $a_1 d_1 e_1 h_1$); on looking into a hollow body matters are reversed (the right eye then occupies the point of view L, and $bcfg$ is smaller than $adeh$). The fallacious impression obtained in such a manner by exchanging two stereoscopic images is designated 'pseudoscopic.'

The pseudoscope, Fig. 37, is an apparatus by which the two eyes which are contemplating an object are subjected to a pseudoscopic influence; each eye receives, namely, by reflexion from the hypothenusal surfaces of a rectangular prism, the impression which belongs to it, reversed, so that one eye receives the form which properly pertains to the other. The body thus appears hollow and as if seen from the inside, when, in reality, its external surface is directed towards the eye, and conversely. The apparatus, as may readily be understood, can only be employed in looking at bodies which are symmetrically formed.

Fig. 37.
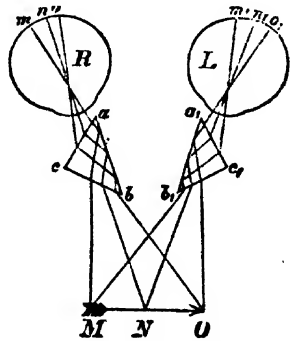
Very distant objects, *e.g.* those parts of a landscape which lie near the horizon, appear usually as if they were extended upon a surface, as in a picture, because the two eyes are situated too close to one another to obtain essentially different views of objects in the distance. The *telestereoscope* of Helmholtz is an instrument which serves to magnify the distance between the points of view of the two eyes. It is a Wheatstone's stereoscope, the two images of which, L and R, are received by two mirrors turned towards the horizon and parallel to the in-

ternal mirrors: the two eyes thus obtain views as if they occupied the positions of the external mirrors, and the horizon appears, consequently, as if it had *stood-out* more; ordinarily the two internal mirrors are looked at through two telescopes.

When two stereoscopic representations of an object are coloured of different intensity (*e.g.* one being black, another white, or of a different colour)—or if two surfaces possessing different depths of the same colour, or coloured differently, be brought before the eye, the object or the surface appears to *shine.* The most probable explanation of this phenomenon is the following:—A surface which is looked at with one eye appears shining, when it reflects the light very uniformly; even absolutely plane or absolutely planely curved surfaces (if presenting no unevennesses) therefore appear *shining.*

If this same surface be examined with the two eyes, it appears to each as possessing a different brilliancy and a different depth of tint, because the reflected light falls into the two eyes at a different angle. If now, conversely, the two eyes receive two impressions which when seen alone are dull, but if they are of different depth, consciousness pictures a regularly reflecting (which consequently illuminates the two eyes differently) and brilliant surface (Helmholtz). The two stereoscopic images of a smooth ball, which exhibit the reflexion of light at different places, give rise in the same way to the impression of a shining ball.

It is not so easy to explain the cause of the brilliancy of colours. The simplest explanation appears to be the following: besides arising by simple regular reflexion, certain sorts of brilliancy are generated by reflexion from multiple surfaces placed one behind the other, even when these surfaces are dull. Thus, for example, *metallic lustre* depends upon the fact that a slightly transparent metal not only reflects light from its surface, but also from its deeper layers (Brücke). As now for two different colours at an equal distance, a somewhat different accomodation of the eye is requisite, it appears as if one colour lay a little behind the other, and so the body exhibits lustre (Dove). Moreover, many persons fail to observe the binocular combination of colours, both colours not uniting to form one image, but they either appear alternately or are seen side by side in the field of view ('Wettstreit der Sehfelder').

Estimation of Magnitude and Distance of Objects.

A third useful purpose subserved by binocular vision is the aid which it affords in the determination of the magnitude and distance of external objects. The starting-point for the determination of magnitude is the size of the retinal image. The greater the latter, the greater, *cœteris paribus,* does the object appear. As, however, the magnitude of the retinal image, or what is the same, the magnitude of the visual angle, does not depend merely upon the magnitude, but also upon the distance of the object from the eye (as the visual angle is inversely proportional to the distance), the determination of the magnitude of objects is associated with a determination of their distance. For the latter, the eye by itself possesses a method of estimation, in the effort to accommodate, the magnitude and direction of the effort being appreciated by the muscular sensation in the muscle concerned. In vision with two eyes there is added the important help afforded by the muscular sense of the muscles which move the eyeball, and which inform us to what degree the optic axes have converged.

An object of apparently equal magnitude appears the nearer, 1, the greater the retinal image which it furnishes; 2, the stronger the positive accommodation ; 3, the stronger the convergence of the optic axes. Further helps to the determination of distance are, the intensity of the light, which in general decreases with the distance. Further, the displacement of the object in reference to others seen at the same time, which occurs either when the object itself moves, or when the other objects move, or when the organ of sight changes its place in consequence of movements of the head or of the whole body.

The most direct proofs that the above are the three principal means of estimating the distance or size of objects are the following :

1. The influence of the retinal image scarcely requires proof ; such a proof is, however, that in defective accommodation (in the circles of diffusion) an object seen appears larger than if the accommodation be perfect and the object sharply defined.

2. The influence of the sensation produced by accommodation is most apparent from the fact that a secondary image, however

produced, changes in apparent magnitude when the accommodation changes; and further, that if red and blue fields occupy the same plane, the first appear nearer than the second (Brücke).

3. The influence of the convergence of the axes is proved in a striking manner by the so-called 'carpet-phenomenon.' If whilst one is looking at any regular pattern (as a carpet) the eye be fixed upon a point lying in front of or behind it, the pattern soon appears to advance in the plane of the point of convergence of the visual axes, and appears, consequently, near or more distant, and in the same manner smaller or larger.

The explanation is easy. Under these circumstances an irregular pattern would appear double; even a regular pattern will appear double; but as in the two images situated one over the other, equal parts of the pattern almost exactly cover one another, the deception originates that both images with their corresponding parts fall upon corresponding points, and therefore the object lies at the distance of the point of intersection of the visual axes (H. Meyer). Just as the images of the centres of the two retinæ are transferred to the point of intersection of the visual axes, so the remaining images are transferred to the surfaces, in which the identical meridians intersect, *i.e.* to the normal surface.

The Organs which protect the Eye.

1. The eye, which is protected nearly on all sides by the osseous orbit in which it is placed, can also be shut off anteriorly by the closure of the cartilaginous eyelids. The closure is effected by the contraction of the *orbicularis palpebrarum* muscle, which receives its nervous supply from the facial nerve, and in so far as the upper eyelid is concerned, it is brought about to a certain extent by the mere action of its weight (gravity). The lower eyelid is opened by the action of gravity, the upper by the contraction of the levator palpebræ superioris, which derives its nervous supply from the third (oculomotor) nerve, whilst both are influenced by *retractor* involuntary muscular fibres which are under the influence of the sympathetic (H. Müller, Sappey). Movements of opening and of closure are frequently and alternately occurring (blinking, winking).

The closure of the eyelids occurs, 1, voluntarily; 2, involuntarily and automatically, in sleep; 3, by reflex action, when the eyeball is touched or the eyelashes which serve as touch-hairs, or when the optic nerve is excited by intense light. The narrowing of the space between the eyelids and the shade thrown by the eyelashes co-operates with the contraction of the pupil in protecting the eye when the light is intense.

The retractors of Müller are situated in the posterior surface of the eye-lids perpendicular to the opening between the lids. Another smooth muscle bridges over the inferior orbital fissure and by its contraction somewhat diminishes the capacity of the orbit, so that the eyeball somewhat projects. Both muscles exist in a state of tonic contraction. When the sympathetic is cut cross in the neck the space between the lids narrows and the eyeball is somewhat retracted (H. Müller).

2. The anterior surface of the eye is continually bathed in lachrymal fluid, and by it maintained in a state of cleanliness and preserved from desiccation. The tears reach it through the fine excretory ducts of the glands situated in the upper and external region of the conjunctival sac. (The conjunctival sac is, as is well known, a mucous sac, which by its free border is attached along the edge of the lids, and which covers a part of the eyeball; it covers the posterior surface of the eyelids, then is reflected over the eyeball, of which it covers the anterior third. The eyelids being closely applied to the eyeball, the conjunctival sac possesses only a capillary lumen. It only widens near the line of contact of the closed lids, where it forms a shallow three-sided canal, as the more slight curvature of the lids does not here permit of their clasping the eyeball). The tears are sucked into the capillary conjunctival space by capillary attraction, and are pressed towards the inner angle of the eye. This movement is aided by the closure of the lids, which presses them towards the inner angle of the eyes (inner canthus), which is the point of attachment of the orbicularis palpebrarum.

The overflow of tears over the fine edge of the lids is prevented, when the secretion is not exceedingly great (as in crying) by the fatty secretion of the *meibomian glands*. At the inner angle of the eye the tears accumulate into what may be called a little tear-lake ('Thränensee'), where commence the two capillary rigid lachrymal canals with their openings, the 'puncta

lachrymalia.' The nasal duct, into which the ducts lead, and which is protected below in the nasal cavity by a valve opening downwards, dilates superiorly at the time when the eyelids are closed (because its posterior wall is connected with the bone, and its anterior with the anterior palpebral ligament which stretches when the lids are closed); by these arrangements it sucks the tears from the little tear-lake. The same effect is produced by the contraction of Horner's muscle, which also enlarges the lachrymal sac.

The closure of the lids might also, when the lids are completely closed, press the tears into the sac. This has actually been recorded to occur by some (Rose, Stellwag, v. Carion). Experiments with coloured fluids, which have been instituted to decide this question, have not furnished concordant result (Stellwag, Arlt).

3. The eyebrows are supposed to protect the eye from the sweat which may flow from the forehead.

Appendix.—The facetted eyes of insects and crustacea are composed of conical segments arranged as the radii of a ball: each of these segments consists of a dioptric apparatus which acts as a convex lens, and of internal nervous structures which are in connection with the terminal ends of the optic nerve in the centre of the ball. Each of these radiating segments, which by pigment and by total reflection (like the rods of the retina) are optically distinct one from the other, most probably only allows such light to be perceived as falls in the direction of its axis, so that the creature possesses, especially for near objects, as many fields of view as there are segments. The adjustment of an optic-nerve element to a particular direction is effected here also, as in the eyes of vertebrata, by other means. In the latter, for instance, the complex dioptric apparatus only allows such light to reach each individual retinal element as follows a particular direction (viz. that of the corresponding visual ray); in the eye of insects, on the other hand, each retinal element has a telescope arranged for one particular direction.

II. THE ORGAN OF HEARING.

Schema of the Organ of Hearing.

The terminal organs of the auditory nerve are spread out like those of the optic nerve on membraneous surfaces, which have, however, an irregular form (*ampullæ, saccules of the vestibule, and membraneous portion of the lamina spiralis*). The sonorous vibrations capable of exciting the auditory nerve are transmitted to these terminal organs by a system of easily vibrating bodies in contact with each other, the first of which, situated most externally, vibrates in unison with the sounding body ; the vibrations of the sonorous body are transmitted to it directly or indirectly : in the latter case through an intermediate body, such as air or water.

There are two such systems, and these have one part in common,—that adjacent to the end organs, viz. the fluid contents of the labyrinth in which the terminal organs are bathed. The labyrinth-fluid can be thrown into vibrations in two ways: 1, by the surrounding bones,—the petrous portion of temporal and all the other cranial bones. This mode of transmission comes into play when the sonorous (solid) body is either in immediate contact with the skull or is connected with it by a chain of solid or fluid bodies, or when the medium immediately surrounding the head is not gaseous, as, for instance, when the sounding body is in contact with the teeth, or when the head is immersed in water ; 2, by the *membrane of the fenestra ovalis*, which separates the labyrinth-fluid from the air-containing tympanic cavity. This membrane is thrown into vibrations by the following chain of bodies (beginning from the fenestra ovalis): *stapes, incus, malleus, membrana tympani*, the *air* and *walls* of the *external meatus* and *auricle*. This system serves for the perception of those sonorous vibrations which are transmitted to the ear by the air : it is therefore the common form of conduction in man, and is found absent in aquatic animals.

Of the two systems just enumerated the latter alone requires further consideration, for the first plays in the case of man only a very infeɩior part.

Conduction of Sound to the Tympanic Cavity.

It is chiefly at the surface of the membrana tympani, but also at the walls of the auricle and external meatus, that the transition of the sonorous vibrations from air to solids takes place. The vibrations communicated to the auricle and external meatus are for the most part conducted further to the membrana tympani along its ring of attachment ; a portion of these reaches the labyrinth through direct conduction by the bones, together with all those vibrations which are imparted to the head by the air. The walls of the external meatus, and possibly also of the auricle, serve, however, a much more important service, by reflecting the sonorous waves on to the membrana tympani, the waves being thrown from the auricle into the auditory meatus and from the meatus on to the membrana tympani. For the auricle, this function is far from proved, and experiment throws great doubt upon it.

There is no form of solid body more adapted for the reception and further transmission of vertically or obliquely impinging air-vibrations than that of a stretched membrane or of rigid, elastic, thin plates. To the latter description the cartilaginous auricle answers, whilst the membrana tympani is of the first-described form. In both cases the body is so thin that the waves of condensation and rarefaction of the air which fall on it are capable of setting *its total mass* in vibration, in the direction of its transverse diameter (transverse vibrations) : otherwise the different layers of molecules would vibrate successively and thus give rise to condensation and rarefaction waves in the body itself (longitudinal vibrations) ; in the first case, where the elasticity has only to be overcome, the resistance is much less and the elongation of the vibrations therefore much greater than in the latter case, where the greater resistance is opposed to the mutual separation of the molecules. Such bodies, however, are also capable of longitudinal vibrations, when vibrations are communicated to them from the border, as *e.g.* the vibrations transmitted to the membrana tympani by the external meatus.

The *reflexion* of sound by the walls of the external meatus requires no further elucidation, for all vibrations which fall on the walls of a cylindrical tube must reach, after being once or oftener reflected, the surface which closes the tube (in the case of the ear, the membrana tympani, which is placed obliquely to the axis of the tube, passing from below upwards, and outwards).

Reflexion of sound waves from the surfaces and promonotories of the

auricles on to the orifice of the auditory meatus may very well be thought possible, especially as the auricle, both *in toto* as well as in its separate parts, is movable by means of muscles (which, however, owing to non-use, are often but ill developed). Experiments, however, in which the whole auricle, with the exception of the meatus (which was prolonged by means of a tube inserted into it) was filled up with a soft material, showed no perceptible diminution of the hearing, from which the function of the auricle as a reflector of sound would seem improbable (Harless) ; others, however, have obtained opposite results (Schneider). The absence of the auricle has not been known to cause diminution of hearing. Artificial reflectors of considerable power (for people affected with difficulty of hearing) are *ear trumpets*, which may be considered to be cylindrical prolongations of the meatus, with a funnel-shaped external termination. The *stethoscope* may be considered as a similar prolongation of the meatus, the other end of which is in contact with the sonorous body ; its action, however, depends, to a great extent, on the conduction of sound along its walls.

Stretched membranes, just like stretched strings, are, in general, only thrown into vibration when the number of their vibrations is the same as, or a multiple of, the number of vibrations of the excited sound, and then they answer only in their own pitch ; the membrana tympani, however, is set in vibration by a sound of any pitch (within certain limits) and vibrates exactly in the proportion of the number of vibrations of, and with an intensity proportional to that of, the sound. Even very complex sonorous waves—compound tones—throw the membrana tympani into fully sympathetic vibration. This is proved by the fact that (within a certain limit) we hear a sound of any given pitch in its own specific timbre and that we are able to judge of its intensity. It must, however, be observed that low tones are heard less distinctly than very high tones of the same objective intensity, showing that the membrana tympani does not respond so well to deeper tones. The peculiarity of the membrana tympani just spoken of is explained as follows : 1, its connection with the ossicles of the ear and the membrane of the fenestra ovalis offers a pretty considerable resistance to its vibrations (Seebeck). This diminishes considerably the intensity of the vibrations of the tympanic membrane (the terminations of the auditory nerve must therefore be very sensitive, Ludwig), but as its mass (and therefore likewise the momentum of inertia) is but small, the influence of its own vibrations is almost entirely lost.

The same circumstance prevents also the continued or after-

vibrations of the tympanic membrane, so that we hear the sound no longer than it lasts; 2, partially also because the state of tension of the tympanic membrane can be altered by the *m. tensor tympani*; this can only make the tympanic membrane answer better to certain tones, *i.e.* to very high or very low tones. Tension of the membrane corresponds to accommodation for high, relaxation of the membrane for low, sounds. A high degree of tension reduces, moreover, the intensity of the vibrations, that is, produces difficulty of hearing (J. Müller), for the resistances are thereby increased.

The stretching of the tympanic membrane by the m. tensor tympani is effected in the following way: the manubrium of the malleus is inserted between the lamellæ of the membrane in a radial direction passing from above downwards and terminating a little below the centre of the membrane. The malleus (together with the incus) is movable around an axis passing through its neck from before backwards (see below), and in its position of equilibrium, owing to its connection with the other ossicles and the elasticity of its supporting ligaments (see below), the lower end of the manubrium points inwards; this causes the membrana tympani to be drawn inwards towards the tympanic cavity in the form of a flattened cone or funnel, the meridians of which, owing to the tension of the circular fibres, are not straight, but somewhat curved, with the convexity outwards.

This form of the tympanic membrane has the advantage of increasing the force of its vibrations at the expense of their amplitude, for it can be proved both mathematically and experimentally that the effect of the atmospheric pressure on the termination (the umbilical central depression of the tympanic membrane) of slightly arched meridians, is the same as if that termination were the end of a very small lever arm, while the atmospheric pressure acts on a very long lever (Helmholtz).

The tendon of the tensor tympani, which, after passing over its pulley and running at right angles to the manubrium, inserts itself into the point of rotation of the malleus, draws with every contraction of its muscle the manubrium still more inwards, and thus brings about a still further tension of the tympanic membrane. The contraction (dependent on the fifth nerve) can be produced by some persons voluntarily (J. Müller); it is observed in all persons as a co-ordinate movement in connection

with the forcible contraction of the muscles of mastication (Fick). Opinion is as yet divided as to whether the contraction is purely a voluntary one or a reflex action (to damp strong impressions of sounds), dependent on the auditory nerve or the sensory nerves of the external meatus. As soon as the contraction of the muscle ceases, the manubrium and, with it, the tympanic membrane, return to their position of equilibrium by help of the elasticity of the membrane, and the arrangement of the ligamentous appendages of the malleus and the connection of the different joints of the ossicles. It will be evident that there is no necessity for a muscle acting as an antagonist to the tensor tympani, and what has been described as such (*laxator tympani*) is merely a ligamentous band.

Many persons can produce at will a crackling noise in the ear, which formerly was thought to be connected with the contraction of the tensor tympani (muscular sound or sudden stretching of the tympanic membrane). This assumption is contradicted by the fact that the sound is not accompanied by a drawing inward of the membrana tympani (this is ascertained by inserting a manometer into the meatus, Politzer, Löwenberg). This sound is now thought to be produced by the sudden opening (by the *tensor palati*) of the Eustachian tube, which, according to some (Toynbee, Politzer, Moos) is considered to be quite closed while at rest, while according to others (Rüdinger, Lucae) it is said to have always a free lumen, which only closes during the act of deglutition (Cleland).

The tympanic membrane can be more powerfully stretched in another way, when, namely, to the already existing conditions there is added a difference of the atmospheric pressure on the two sides of the membrane (in the tympanic cavity and in the external meatus). Ordinarily the atmospheric pressure is the same on both sides, for the air in the tympanic cavity, which is connected with the pharynx through the Eustachian tube, is under atmospheric pressure. By a forcible expiration the oral and nasal cavities being closed, air can be driven into the tympanic cavity, whilst by a forcible inspiration, under the same conditions, air will be driven from that cavity (Valsalva's experiment). In the first case the tympanic membrane will be driven outwards, in the latter case inwards, and in both cases therefore it will be more stretched. The consequence of this is, besides the accommodation for higher pitched sounds, a momentary deafness. Permanent deafness is caused when by

occlusion of the *Eustachian tube*, the atmospheric pressure in the tympanic cavity is abnormal, a condition which can only be remedied by making the *tube* permeable (introduction of a catheter through the inferior nasal passage).

The lowest sounds which can still be perceived are said to be those of 40, the highest those of about 16,000 vibrations in the second; it is however doubtful whether this limit is due to the tympanic membrane, or to the perceptive power of the auditory nerve. The limits are different for different persons; thus some persons can hear some high-pitched sounds and yet not perceive still higher pitched sounds audible to others, as, *e.g.* the chirping of the cricket. (Compare also what is said further on on the different forms of vibrations of the tympanic membrane.)

Conduction of Sound by the Tympanic Cavity.

The further conduction of the vibrations of the tympanic membrane is affected by the chain of ear ossicles, which appear only to serve the purpose of transmitting the vibrations of the tympanic membrane to the membrane of the fenestra ovalis.

In birds, and in the scaly amphibia, they are therefore represented by a single rod-like ossicle (*columella*) only. In man the two opposed membranes are not connected by a single rod, but by a compound lever composed of three bones, the axis of rotation of which is the malleo-incus axis (a, in Fig. 38).

Fig. 38. · The arrows in the figure · indicate how the membrane of the fenestra ovalis must always vibrate in the same sense as the membrana tympani. The connection of the lever with the membrane of the fenestra ovalis is not brought about, as in the case of the tympanic membrane, by a radially inserted arm, but by a plate, which is attached centrally, *the base* or *foot* of the *stirrup*. The joints between the separate ossicles, which are so fixed by help of their own elasticity and the contraction of the tensor tympani, that their system vibrates as a whole with the tympanic membrane, serve most probably to allow the mutual sliding of the ossicles in the different positions of the membrana tympani, for which purpose also the stirrup is attached by its base, so as to be able to vibrate only in the direction of its slightly moveable longitudinal axis. The dimensions of the ossicles and the amount of the fluid of the labyrinth
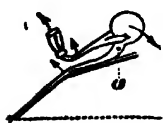
which vibrates with them, are so small in comparison to the wave length of the sound waves, that all these parts must always be in the same *phase* of vibration. (E. Weber, Helmholtz.)

The malleus is supported by a ligamentous mass which is stretched from before backwards through the tympanic cavity, forming at the same time the axis of rotation (axial band, Helmholtz); this band consists of two ligaments, which are inserted into the neck of the malleus, an *anterior ligament*, attached to the spina tympanica anterior, and a *posterior ligament*, which is only a prolongation of the anterior. The movements of the membrana tympani being communicated to the manubrium of the malleus, the latter, and with it the incus, rotate round the axis just described; the incus is chiefly supported by the malleus, but it is so connected by its short process to the posterior wall of the tympanic cavity, that it slightly modifies the movements of the malleus (so that both might be considered as forming one complex lever), and allows the umbilicus of the tympanic membrane to move only in a direction vertical to the marginal plane of the membrane. The long process of the incus, which articulates with the stapes, curves round a little inwards from the manubrium of the malleus, remaining throughout parallel to it. The articulation between malleus and incus is saddle-shaped, the body of the incus surrounding the convexo-concave articular surface found on the neck of the malleus. The articular surfaces are provided with a kind of *check tooth*, so that only the rotations inwards of the malleus are exactly communicated to the incus, but not the rotations outwards; from this it follows that the stapes cannot be torn away from the fenestra ovalis by such outward movements of the tympanic membrane, while the tension of the latter membrane provides against the forcing in of the stapes (Helmholtz). The action of the stapedius muscle, which, passing from behind and at right angles to, inserts itself into the constricted portion of the neck of the stapes, seems to be that of altering the position of the foot of the stapes in its relation to the membrane of the fenestra ovalis, the foot being either pushed in by its posterior border or lifted out by its anterior border; both movements, it is presumed, diminish the amount of excursion of the stapes; the stapedius muscle would thus act as a damper. Nothing definite is known about its innervation (by the *facial nerve*).

The lever formed by the malleus and incus, the fulcrum of which is at the end of the short process of the incus, transfers the vibrations of the tympanic membrane to the stapes, diminished in extent in the ratio of 3 : 2, but inversely increased in force, an arrangement which, considering the great resistance to the stapes, can only be of advantage (Helmholtz).

Conduction through the Labyrinth.

The impulses of the base of the stapes produce progressive waves in the labyrinth, *i.e.* the fluid contents of the labyrinth recede in toto with every impulse, thereby causing the yielding part in the wall of the labyrinth, the *fenestra rotunda*,

to arch outwards towards the tympanic cavity. (If the labyrinth fluid were surrounded on all sides by rigid walls, each impulse of the foot of the stapes would, to a large extent, be reflected, and only an infinitesimal part of the kinetic energy would be propagated through the nearly incompressible labyrinth fluid, in the form of waves of condensation and rarefaction.) The further course of the wave produced by the impulse of the base of the stapes in the labyrinth, and whether all parts are equally set in motion and so on, can, in consequence of the complicated form of the labyrinth, only be surmised. The last part of the course, namely, that through the *Cochlea,* is best known. The wave entering by the *apertura scalæ vestibuli* runs along the *scala vestibuli* to the cupola, passes thence into the *scala tympani,* which it traverses to its end, viz. to the *fenestra rotunda;* it is, however, highly probable that already during its course along the *scala vestibuli* a partial passage into the scala tympani takes place through the *lamina spiralis membranacea.* Much more difficult to understand is the course of the wave in the vestibule and the semicircular canals. It seems most natural to assume that the wave, on entering the vestibule, is split up, sending a branch into each semicircular canal, and that all these waves again unite in the vestibule to be transmitted to the cochlea. In its course along the vestibule the wave would move the saccules, and in its course along the semicircular canals, the ridges of the *ampullæ.* The use of the semicircular canals would then rest in this, that they enable the ridges of the ampullæ to be moved, for no to-and-fro wave could enter a perfectly closed cavity. This explanation, however, is far from satisfactory (compare also the Appendix to the Organ of Hearing).

From what has been said, the importance of the air-containing tympanic cavity, namely to give free play both to the vibrations of the tympanic membrane and ossicles and to the deviation of the membrane of the fenestra rotunda, will be evident, the function of the Eustachian tubes being, as already stated (page 433), the equilisation of the pressure in the tympanic cavity with that of the air. The supposition that the tuba serves chiefly the purpose of enabling one to hear one's own voice, is not very probable.

Just as normally the vibrations of the air are transmitted to the vibrating parts of the organ of hearing by the membrana tympani, so the reverse happens, when the organ of hearing is *primarily* (by conduction through bone, as, *e.g.,* in the case of one's own voice) set in vibration; this mode of

conduction diminishes the vibrations of the ear (Mach). By preventing the transmission of vibrations outwards (closing the meatus) the sound of one's own voice, conducted by the bones, is increased (Weber).

Hearing.

Excitation of the Terminal Organs of the Auditory Nerve.

The movements of the liquid contents of the labyrinth, which are communicated to the membranous labyrinth and the membranous part of the lamina spiralis, give rise to auditory sensations by exciting the terminations of the auditory nerve, which are contained in it.

The present state of knowledge as to the terminal organs of the auditory nerve may be stated as follows:—

1. *Nerve-Endings in the Ampullæ and Vestibular Sacs (Sacculus and Utriculus).* — In the *ampullæ* the nerve-endings are contained in a yellowish, semicircular, equatorial septum, which is a thickening of the membranous labyrinth (Scarpa, Steifensand, M. Schultze). Its structure, particularly in the skate, as investigated by M. Schultze, may be thus described. The simple epithelium of the ampullæ is raised on the septum of hard connective tissue, so as to form a thick cushion consisting of several layers, from which fine stiff bristles (the *auditory cirrhi*) project, of such length as almost to reach the opposite wall of the ampullæ. The nerves, which suddenly part with their medullary sheaths at the border of the connective tissue, are distributed in the epithelial mass, breaking up into naked axis-cylinders of extreme fineness.

The cells of the epithelial layer are of the following kinds:—

a. Several layers of cylindrical nucleated epithelial cells, of which the deepest (called '*Basal cells*') are somewhat pyramidal and pointed. *b.* Spindle-shaped cells, each of which has two long fine processes, one of which is directed towards the surface where it seems to end, while the other, which is frequently varicose (these varicosities being, according to Schultze, artificial products), tends towards the base, its mode of termination being uncertain. These spindle-shaped cells, with their fibres, are nervous structures, and are supposed to constitute the ends of the fine axis-cylinders. *c.* Round or cylindrical cells in the superficial layer, each of which sends out one of the auditory cirrhi or hairs already referred to. According to some, these cirrhi spring out of the superficial processes of the nerve cells.

In the vestibular sacs, as observed in fishes, the nerve-endings are in like manner contained in a crescentic septum, which, however, is less elevated. In this structure the same elements are found as in that of the ampullæ, with the exception of the cirrhi, the place of which is taken by the *otolith*. This is accurately applied to that part of the inner wall of the sacculus which bears the septum, for the reception of which it is grooved. The otolith consists of a hard or pasty mass of minute prisms

of calcic carbonate in the form of arragonite, and is suspended without attachment in the viscid fluid resembling vitreous humour (*endolymph*) which occupies the cavity (M. Schultze). Here and there short cirrhi are to be seen where the otolith is not applied to the surface.

2. *Nerve-Endings in the Cochlea (Organ of Corti).*—The special canal which winds round the columella of the cochlea is divided into three channels, viz. the *Scala vestibuli* (*Sc. Ve.* Fig. 39), the *Scala tympani* (*Sc.*

FIG. 39.
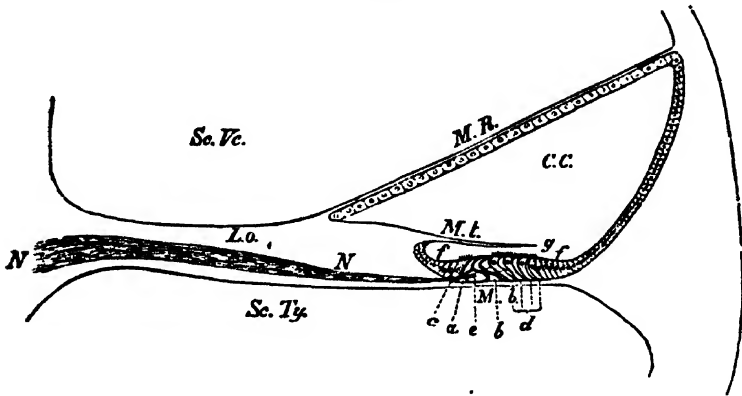
Ty.), and the *duct of the Cochlea* (C.C.) which lies between them—by the bony part of the lamina spiralis (L.O.), and by the two membranes which stretch across from this structure to the outer wall of the canal, namely, the *membrana basilaris* (*M. b.*) and the *membrane of Reissner* (*M.R.*). The fibres of the cochlear nerve, which are contained in the columella, spread out from it in the form of a fan, which winds spirally round it, entering the duct of the cochlea by the radiating canaliculi of the lamina ossea (*N.N.*), in order to reach the *organ of Corti*. This organ, according to the latest researches (Kölliker, Böttcher, Waldeyer and Gottstein, v. Winiwarter), has the following structure:—The epithelial lining of the duct of the cochlea assumes on the membrana basilaris a peculiar development. In every radial section, two hardish elastic pillars (*a* and *b*) are seen, which articulate with each other by their heads. These are called the '*arches or pillars of Corti.*' On the inner side of each internal pillar, an '*internal hair cell*' (*c*) is to be found, which is in connection with the nerve fibre. In like manner, on the outer side of the outer pillar, there are a number of '*external hair cells*' (*d*). These (which in mammalia generally are three in number, but in the human cochlea four or five, while in birds and amphibia they are wanting) are also provided with nerve fibres (*e*). The heads of the pillars of Corti have each of them a process by which it contributes to the formation of a supporting network (the *lamina reticularis*), the level of which coincides with that of the epithelial border (lamina reticularis, *f. f.*). In the rings of this beautiful network, the heads of the hair cells fit in quincuncial arrangement. The whole organ of Corti is covered by a soft membrane (*M. t.*), which springs from the lamina ossea, and floats by its free edge (*g*) in the fluid of the cochlear duct. (The drawing is diagrammatic.)

In all the organs of the internal ear there are arrangements in connection with the nerve-ending, of such a nature as to favour their *mechanical* excitation. Thus, in the ampullæ, and in the organ of Corti, the cirrhi, thrown into motion by the passing wave of liquid, may agitate the nerve cells; in the vestibule the nerve-endings, to which the otoliths are most accurately applied, must be tapped by them on the slightest agitation; while, finally, throughout the whole membrana basilaris of the cochlea, the vibratious of the membranes and pillars must exercise pressure on the nerve cells wedged in between them. Hence arises the notion that the excitation of the auditory nerve-endings consists in their being mechanically tetanized—a notion which seems to be supported by the constant occurrence of otoliths throughout the whole animal kingdom.

At present we have only hypotheses as to the special functions of the various terminal organs, and consequently of the various parts of the labyrinth. The opinion formerly held, that the cochlea serves specially for the perception of auditory impressions transmitted through bone, rested on the mistaken assumption that the nerves of the cochlea ended directly in the lamina ossea. Such a view is negatived by the existence of the organ of Corti, and by the absence of the cochlea in animals which only hear by conduction through bone, *e.g.* in fishes. Further information as to the probable function of the cochlea will be given below. With reference to the semicircular canals, see the Appendix to this Section.

Characteristics of the Sensation of Hearing.

The excitation of the terminal organs of the auditory nerve by the vibrations of the liquid contents of the labyrinth, or any other excitation of the auditory nerve fibres, causes an auditory sensation. The 'height' (elongation) of the waves determines the *intensity* of the perception of sound, while the 'length' of the waves, or the number of the vibrations in a given time, determines the *pitch* of the tone heard.

As regards pitch, the range within which sounds can be distinguished is very considerable, and the limits given on p. 393 are probably determined, not by the excitability of the auditory nerve, but by the vibratory capacity of the transmitting organs, *e.g.* of the tympanum.

The interval between the lowest tone there given (40 vibrations) and the highest (16,000 to 20,000) amounts to $8\frac{1}{2}$

or 9 octaves, whereas the interval between the limits of visibility of the red and violet rays reckoned in an analogous manner does not reach one octave.

The subjects of auditory sensations are generally, however, not simple tones, just as the colours we usually see are not the simple colours of the spectrum, but mixed colours. Ordinary sounds consist of musical tones, simple or compound, or of noises.

The essence of a compound musical sound, and its analysis into simple tones, has been already discussed (p. 303). Simple tones can only be artificially produced by throwing a resonator into consonance with one of the constituent or partial tones of a compound tone, with which tone it is in tune. For such a purpose one of the resonators mentioned on p. 303, or the resonance tubes (p. 314), may be employed; or a monochord, along the string of which a vibrating tuning-fork is made to slide until the string is of such length that its 'proper tone' is in unison with a constituent tone of the compound sound produced by the tuning-fork (Helmholtz).

If two different simple tones of a given force are produced simultaneously, mutual disturbances in their wave-systems become perceptible, which give rise in sound-conducting media—*e.g.* the air—to new vibrations.

These new vibrations are of two orders, in one of which the vibration number is equal to the *difference* between the two primary vibration numbers, and in the other to their sum. Although in this case only one resulting wave-system reaches the ear and is transmitted unchanged through the conducting media to the nerve-endings, *four separate single tones are heard at the same time,* provided the intensity is sufficient; that is to say, two primary and two *combinational tones.* Of these last, one is the *differential tone,* the other the *summational tone.*

Whenever a compound tone is produced we recognise in it its specific composition—in other words, the *musical colour* (*Klangfarbe*), *timbre* or 'quality,' which accompanies the fundamental tone. (See p. 302.) Besides this, each single constituent tone of the compound tone may, without special practice, be singled out from it by the ear, provided that immediately before the production of the compound tone the single tone has been heard.

Finally, the effect produced by the simultaneous sounding of many compound tones is not, as one might expect from the complexity of the resulting wave-systems which pass through the

ear, a mere noise, for each separate tone can be clearly dis-
tinguished. Indeed, in an orchestra, one instrument can be
singled out from the rest, and its sounds followed.

All these observations point to the conclusion· that there is
in the organ of hearing an *arrangement which resolves every
wave-system, however complex, into simple pendulum vibra-
tions;* just as every compound tone may be resolved by reso-
nators into its constituent tones. They indicate further that·
every simple partial vibration excites a particular nerve fibre,
and by doing so brings about the sensation of a simple tone.
This supposition, the only one which satisfies the principle of
specific energies (p. 343), is raised into a certainty by the
following observation (Helmholtz): If several simple tones,
each beginning at a different time, in such a way that. different
phases of their vibrations are coincident, are combined into one
compound tone, the most manifold variations of the combined
wave-system result. If the auditory nerves were excited to
different forms of functional activity by the wave-system as
such, then the impressions of musical sounds received would
vary in each experiment. But if the experiment is made with
the vowel apparatus mentioned on p. 314, it is found that in all
cases the same musical sound is heard; the slightest difference
would manifest itself in a corresponding difference in the vowel
sound.

Every resonator answers, not only to its proper tone, but also to tones
which are very near it; the further, however, the two tones are apart, the
feebler is the resonance.[1]

The difference as regards pitch, at which a resonator is capable of being
excited by a tone (called the range of sympathetic vibration) varies
proportionately to the completeness with which the resonator is damped.
The degree of damping is measured by the number of vibrations which
must occur before the intensity is reduced to a definite fraction—say to one-
tenth of what it was at first. On the other hand, the extent of the sympa-
thetic vibration executed by any tone can be measured by the difference
between this tone and the proper tone of the resonator when the former
excites the resonator, as its proper tone does, but with a definite fraction,
say, one-tenth of its intensity. If this difference is known, the degree of
damping of the resonator can be calculated, and *vice versa.* The following
Table shows the relation in which each stands to the other (Helmholtz):—

---

[1] In point of fact, the strongest answering tone is somewhat different from the
proper tone of the resonator; the two would only be absolutely identical, if
friction and resistance of the air were nil.

Difference of pitch (the intensity of the sympathetic vibration being reduced to one-tenth).	Number of vibrations which occur before the intensity of the tone of the resonator is reduced to one-tenth.
Eighth of a Tone	38·00
Fourth of a Tone	19·00
Semitone	9·50
Three-fourths of a Tone	6·33
Whole Tone	4·75
Five-fourths of a Tone	3·80
Tempered Minor Third (1¼ Tone)	3·17
Seven-fourths of a Tone	2·71
Tempered Major Third (2 Tones)	2·37

The degree of damping of the resonator in the ear may be ascertained by the following experiment:—A shake, of which the beats recur ten times in a second, can be heard with perfect distinctness at all parts of the scale down to the low A (110 vibrations) without the impression of the alternation of the two tones being obliterated in the ear by the after-sounding of the vibrating parts. Below A this is the case. Assuming then that the intensity of the vibrations must sink to one-tenth in order that when the same tone recurs, that is to say, after an interval of a fifth of a second, it is no longer audible, it follows that the parts of the organ of hearing set into vibration by A after a fifth of a second, *i.e.* 22 vibrations, continue to vibrate with only a tenth of their original intensity. The degree of damping of the resonators in the ear must therefore correspond to about the second, or perhaps the third or fourth degree of the Table given above; and it is actually observed that below A the shake becomes rough and confused. Taking the third degree as the correct one, if the intensity of excitation of the resonator, by its proper tone, is equal to 100, its excitation by other tones approximating it in pitch will be as follows :

Difference of pitch in fractions of a whole Tone	0	0·1	0·2	0·3	0·4	0·5	0·6	0·7	0·8	0·9	1·0
Intensity of sympathetic vibrations	100	74	41	24	15	10	7·2	5·4	4·2	3·3	2·7

The parts of the ear which are set into vibration by the note A are therefore affected with only one-tenth of the intensity by any tone which is removed half a tone from A in pitch; hence the same resonators cannot be called into action for A sharp and A flat, as for A. This is another argument in favour of the theory above quoted (Helmholtz).

The occurrence of deafness for a series of tones, *e.g.* the deepest notes (bass deafness), which is frequently observed, favours the opinion that there exist in the ear separate organs for the preception of tones of different pitch (Moos). According to this theory any simple tone would excite the particular resonator in the ear of which the proper tone is nearest to it, with the greatest intensity, those adjoining it, with less.

Theoretical considerations, however, indicate that if the membrana tympani is excited by a simple tone, it vibrates at the same time with

the harmonic overtones of the exciting tone; so that the resonators answering to these overtones are excited, as well as those answering to the original tone, and therefore a simple tone is never heard (J. J. Müller).

The analysis of compound tones in the ear can only be effected by a system of resonators. It is still a matter of conjecture what part of the ear is to be regarded as constituting such a system. The cochlea claims the first consideration in this point of view. If we suppose the arches of Corti to be resonators (Helmholtz), an obvious correspondence presents itself between their gradually increasing dimensions and the graduation required in the numbers expressing their proper vibrations. Or we may take the simpler view that the rays of the membrana basilaris (Hensen), due to the greater tension of the membrane in the radial than in the longitudinal direction, correspond to a series of tense strings of gradually increasing length. According to another view, the auditory cirrhi of the labyrinth and cochlea may constitute a system of which the graduation is dependent on the varied length or stiffness of these organs (Hensen).

According to Kölliker, the cochlea contains about 3,000 arches of Corti. Deducting 200 for tones which are musically unavailable, 2,800 remain for the seven octaves that are musically audible (from C $_{\text{II}}$. to H $_{\text{VI}}$.) Hence there are 400 arches to each octave, and $33\frac{1}{3}$ ($= \frac{400}{12}$) to each semitone. As skilled musicians can distinguish an interval amounting to $\frac{1}{64}$ of a semitone (E. H. Weber), it may be assumed that a tone which is intermediate between the proper tones of two adjoining Corti's elements will affect both with unequal intensity, and that by this difference the pitch will be perceived (Helmholtz).

At least two vibrations following one another with rapidity are necessary to excite the sensation of a tone. A single vibration causes only the impression of a tap. If, for example, a card is held against the teeth of a revolving Savart's toothed wheel, so as to produce sound, the tone is unaltered so long as the rate of revolution remains the same. If, now, all the teeth excepting the last two are gradually removed, the same tone continues to be heard, although it becomes duller, just as a colour becomes duller when mixed with a good deal of 'black.' If the last tooth but one is removed, the tone vanishes and only the sensation of a tap remains, which is to be regarded as a rapidly vanishing wave-system.

If many different simple tones are so combined that the

organ of hearing cannot analyse them, or if they follow each other so rapidly that the after-tones of each preceding tone are mingled with those of its successor, so that a confusion arises which cannot be analysed by the ear, and in which no periodicity can be perceived, the resulting sensation is commonly called a noise. Many noises therefore are only very complicated musical sounds, in which a fundamental or prime tone, having often the timbre of a vowel, can be recognised. According to the vowel sound heard, these noises receive names by onomato-poiesis, such as clinking, thundering, clattering, crackling, &c. Beside these apparently unperiodical sound vibrations (which, however, must needs be possessed of periodicity, seeing that they are composed of tones), there are others which are really un-periodical, and to the impression on the ear of these the term noise should be exclusively applied (Helmholtz). In what parts of the organ of hearing the perception of taps and noises takes place is at present matter only of conjecture without proof. (Ampullæ and Sacculus).

The mingling of successive tones would be much more constant, and music would be therefore impossible, if the damping of the vibrating parts of the ear were not very complete. The damping apparatus has not yet been thoroughly investigated. It has been supposed by some that the otoliths and the *membrana tectoria* of the cochlea, which lies upon the organ of Corti (p. 438), constitute damping apparatus (Waldeyer).

Harmony of Musical Sounds.

If several musical sounds reach the ear at the same time, an agreeable or disagreeable impression is received, the nature of which is ultimately connected with the relations of the vibrational numbers of their prime tones. According to these relations we distinguish consonant (agreeable) and dissonant (disagreeable) combinations of sounds. The octave (1 : 2) and the twelfth (1 : 3) are the most perfectly consonant sounds; then follow in order in the direction of dissonance, the fifth (2 : 3), fourth (3 : 4), major sixth (3 : 5), major third (4 : 5), minor sixth (5 : 8), minor third (5 : 6), &c. The explanation of this phenomenon is that the disagreeable impression of a dis-sonance consists in the beats caused by it, *i.e.* in the variations of intensity produced by the interference of two wave-systems which differ somewhat in their wave-lengths. Two simultaneous

tones of different pitch strengthen each other whenever the wave crests or the wave troughs between them coincide, and they weaken or annul each other when crests coincide with troughs. The periods of recurrence of beats must obviously be equal to the difference between the vibration numbers of the two tones; the smaller the interval between the two tones and the lower the pitch, the less frequently do the beats occur. If they are so frequent that they cannot be recognised separately as beats, they give the impression of a painful discontinuity (comparable to the flickering of a light). The maximum of confusion and roughness is experienced when the beats recur thirty-three times in a second. The more nearly the constituent tones of two simultaneous compound tones coincide with each other or with combinational tones (p. 440), so as to give rise to beats of moderate frequency, the greater will be the discord.

For further explanation attention is directed to the Table, which, starting from the prime tone C (256 vibrations), sets forth the vibration numbers of its constituent tones, as well as those of some of the tones derived from it. If all the conditions of dissonance were given, the Table would also exhibit the combinational tones, which are, however, not here taken into consideration. The small figures denote the number of beats which a constituent tone makes with the two constituent tones of the fundamental compound tone (*Grundklang*) which are nearest to it.

It is seen from the Table that in the sounds of the octave and twelfth there are no constituent tones, except those which are also in the fundamental sound; here therefore no beats are possible—the octave and twelfth are in 'absolute' consonance. In the sound of the fifth, constituent tones exist which are not in the fundamental tone, but these are not brought into such collision with those of the fundamental tone nearest to them as to cause beats: the fifth therefore is a 'perfect' consonant. The conditions, however, for beats exist in the constituent tones of the fourth, major sixth and major third ('medial' consonances), and in an even greater degree in those of the minor sixth and minor third ('imperfect' concords), and still more in those of seventh, second, &c. (dissonances). It is also seen that the number of beats gradually approaches 33. Dissonance is occasioned by any interval, the more readily the lower the pitch. (Compare the statement above.) On these principles rest the sciences of harmony and temperament, which cannot, however, be entered upon here. The relation of constituent tones (their 'melodic relationship') is also important with regard to the succession of sounds which constitutes melody. If a sound is followed by its octave, no new tone is heard, the attention is not attracted by

Vibration Numbers of Partial Tones and Beat-Numbers *(beat-numbers shown in italics below each partial)*

Compound Tones	256	512	768	1024	1280	1536	1792	2048	2304	2560	Smallest Beat-Numbers	Degree of Consonance
Prime tone c^{I} 256												
Octave c^{II} 512		512		1024		1536		2048		2560	No beats	Absolute
Twelfth g^{II} 768			768			1536			2304		No beats	Perfect
Fifth g^{I} 384	384 *128*		768	1152 *128 128*		1536	1920 *128 128*		2304		$128 = \frac{256}{2}$	Perfect
Fourth f^{I} 341	341 *85 171*		683 *171 85*	1024	1365 *85 171*		1707 *171 85*	2048	2389 *85 171*	2560	$85\ldots = \frac{256}{3}$	Medial
Major sixth a^{I} 427	427 *171 85*		853 *85 171*		1280		1707 *171 85*	2133 *85 171*		2560	$85\ldots = \frac{256}{3}$	Medial
Major third e^{I} 320	320 *64 192*	640 *128 128*		960 *192 64*	1280	1600 *64 192*	1920 *128 128*		2240 *192 64*	2560	$64 = \frac{256}{4}$	Medial
Minor sixth as^{I} 410	410 *154 102*		819 *51 205*		1229 *205 51*	1638 *102 154*		2048		2458 *154 102*	$51\ldots = \frac{256}{5}$	Imperfect
Minor third es^{I} 307	307 *51 205*	614 *102 154*		922 *154 102*	1229 *205 51*	1536	1843 *51 205*	2150 *102 154*		2458 *154 102*	$51\ldots = \frac{256}{5}$	Imperfect
Major seventh h^{I} 480	480 *224 32*			960 *192 64*		1440 *160 96*	1920 *128 128*		2400 *96 160*	2400 *96 160*	$32 = \frac{256}{8}$	Dissonance

any new impression. The contrary is the case when a note is followed by its fifth or fourth, &c.

If a compound tone, of which the prime tone makes n vibrations in a second, is heard along with others, the smallest number of beats per second depends on the relation between the two tones, as follows:—The fundamental tone in simultaneous vibration with the fifth gives $\frac{n}{2}$ beats, with the fourth and major sixth $\frac{n}{3}$, with the major third $\frac{n}{4}$, with the minor sixth and minor third $\frac{n}{5}$, with the major seventh and major second (a whole tone) $\frac{n}{8}$, with the minor second (semitone) $\frac{1}{15}n$, &c. This may be more generally expressed as follows:—If n represents the vibrational number of the deeper ground tone, and m that of the higher, and the fraction $\frac{m}{n}$ is reduced to the smallest whole numbers $\left(\frac{m^1}{n^1}\right)$, then the minimum number of beats is $=\frac{n^1}{n}$. In other words, the smaller n is (that is, the lower the pitch) and the greater n^1 is (that is, the more incommensurable the fraction which expresses the interval), the smaller is the minimum number of beats per second.

The fraction $\frac{m^1}{n^1}$ is clearly $\frac{3}{2}$ for the fifth, $\frac{4}{3}$ for the fourth, $\frac{5}{3}$ for the major sixth, $\frac{5}{4}$ for the major third, $\frac{8}{5}$ for the minor sixth, $\frac{6}{5}$ for the minor third, $\frac{15}{8}$ for the major seventh, $\frac{9}{8}$ for the major second, $\frac{16}{15}$ for the minor second.

A simple experiment shows convincingly that the essence of dissonance really lies in the beats. If one of two perfectly similar tuning-forks, standing on resonance cases, is put more and more out of tune by means of wax, beats of increasing frequency are heard on sounding them; when those beats reach a certain rate of frequency the characteristic sensation of discord is perceived.

Hearing from Outside.

The cause of every sensation of sound which is transmitted by the membrana tympani appears to the mind to come from outside, whereas that which is conducted through bone appears to arise in the head itself. If, *e.g.*, the head is held under water the impressions of hearing will only seem to come from outside when the external ear is filled with air (Weber). As, however, even in this case the principal conduction is by means of the bones in the head, the impression of extrinsic origin is occasioned by the sensibility of the membrana tympani, and is not due to any particular form given to the labyrinth waves emanating from the stapes. If this be so, one may suppose that the sensibility of the membrana tympani gives information as to the direction of the sound-waves which reach it, and perhaps this is also the case as regards the pinna, which from its numerous projections is peculiarly adapted to judge of the angle at which the sound rays fall (Weber), especially when it is aided by its movements. (Compare what follows.)

Subjective Sensations of Hearing.

In the organ of hearing, as in that of sight, there are certain 'subjective sensations,' which depend either upon peculiarities in the excitation of the nerve, or upon abnormal conditions of the nerve itself. These impressions, however, appear to be of very limited occurrence, and have been as yet but little investigated. With reference to after-tones, it may with probability be concluded that when a series of tones succeed each other with rapidity (as, for example, when the teeth of a Savart's wheel are so set that instead of being equidistant throughout they are at different distances from each other in successive segments of the circumference), a noise is produced by the mixture of tones which is analogous to the mixture of colours in the colour top (p. 401). 'After-sounds' are to be regarded as physical phenomena, as for example when a tone or a piece of music rings in the ear long after the sound has ceased to be actually heard. This is also true of other hallucinations of hearing.

Amongst subjective impressions may be mentioned ringing and humming in the ears. These tones or noises are dependent upon the excitation of the auditory nerves by unknown causes, and are particularly apt to occur when their excitability is morbidly increased. The subjective musical tones which are occasionally observed may probably be explained as arising from abnormal excitation of the nerve fibre corresponding to a single element of the organ of Corti (p. 438); for in these cases there is at the same time excessive sensibility to the objective sounds which correspond to those heard subjectively (Moos, Czerny, Samelson). The buzzing which is heard when the auditory passages are closed is dependent on the fact that under this condition we hear principally by conduction through bone; consequently the muscular sounds of the head, and the friction sounds produced by the circulating blood, are perceived.

Entotic Impressions.

From subjective sensations may be distinguished those impressions which have their source in the organ of hearing, and are therefore called *entotic*. To these belong, 1, rushing sounds caused by vibrations of the air in the external ear, or in the cavity of the tympanum, when their communication with the atmosphere is interrupted—in the case of the former by substances covering it, or inserted into it, or by cerumen; in that of the latter, by occlusion of the Eustachian tube. These sounds in the external ear are particularly loud when a hollow body, such as a tube, in which the air vibrates, is applied to the auditory passage, so as to lengthen it. 2. The crackling sound caused by contraction of the tensor tympani, as to the significance of which see p. 433. 3. Hammering sounds, caused by the pulsation of the arteries either in the organ of hearing, or at a distance from it. These become more audible when the head rests upon a hard body. 4. Friction sounds, caused by the circulating blood. 5. Muscular sounds, &c.

Hearing with both Ears.

By hearing with both ears, as by seeing with both eyes, the two organs are enabled to assist each other mutually and to correct each other's errors. We are also thereby aided in determining the locality of sound-producing bodies. Whether the terminations of the organ of hearing possess anything corresponding to the 'identity' which exists in the eyes, whether, for example, the excitation of two corresponding fibres of both cochleæ is perceived as a single sensation, cannot at present be decided. A single tone, although it is heard by both ears is heard only as one, in which case we may assume that the elements in the two cochleæ which are affected by it correspond with each other. On the other hand, we can distinguish two tones even when both ears are excited simultaneously by tones of the same pitch, provided that either their intensities are different or that the excitability of the two corresponding elements is unequal. This last statement is proved by the following experiment. If two similarly sounding tuning-forks are held one before each ear, and one of them is made to revolve round its axis in such a way that the tone shall alternately vanish and reappear (four times in one revolution), neither fork is heard continuously, but both sound alternately, the fixed one being only audible when the revolving one is not heard (Dove). The excitability naturally diminishes during the continuance of the sound, but less on the side of the revolving tuning-fork than on the other side. If the excitation is of equal intensity, the impression of a tone will be perceived only on the side on which the excitability is greater. (This result is of course not obtained when the two tones are different.) From this experiment it may be concluded either that the excitations of two corresponding elements of both ears can be distinguished from each other, or that the excitation is perceived as a single one, but is referred to the side on which the excitation is strongest. Both conclusions are opposed to the admission of an analogy with the organ of sight. The value of the experiment is, however, diminished by the circumstance that in all probability the sounds of the two forks are not absolutely identical. Another fact which appears to militate against the notion that we perceive excitations of both ears in common, is that in most persons (Fessel, Fechner), and especially in pathological conditions

(v. Wittich) one ear perceives the same tone at a higher pitch than the other.

Appreciation of Direction.

Two opposite membranæ tympani and pinnæ must naturally afford a more accurate indication of the direction of a sound than one alone, considering that by turning the head we can alter the relation of the ears to the sounding body. It is indeed conceivable that the different local relation of the two ears to objects might enable us to judge of distance.[1] The position of the ears is best adapted for the discrimination of sounds coming from the sides. Those from before or behind can only be distinguished by turning the head or by the position of the pinnæ the situation of which is best adapted for the reception of waves coming from the front. These are therefore heard more loudly than those from behind. If the pinnæ are pressed against the head and the hands placed before the external meatus, so as to form a kind of ear, sounds coming from behind are heard more loudly than they would be otherwise.

Protective Organs of the Ear.

In a certain sense the pinnæ, especially in animals where they are mobile, may be regarded as protective organs for the ears, inasmuch as the existence of projections (*e.g.* the tragus in man) tends to hinder the penetration of dust or cold air into the ear. Other protective organs are the stiff bristly hairs (vibrissæ) of the external meatus, and the ceruminous glands, the secretion from which lubricates the wall of the meatus. The purpose of the cerumen is uncertain. Its absence determines difficulty of hearing and buzzing in the ears, the cause of which is unknown. The internal ear, from its position inside the petrous bone, is completely protected.

APPENDIX.—Destruction of the membranous labyrinth (Flourens), as well as section of the auditory nerve (Brown-Sequard) in animals, cause striking rotatory movements of the head, abnormalities of the movements of locomotion, and movements which resemble the uncontrollable rotations (*Zwangsbewegungen*) which occur after certain injuries of the brain (Chap. XI.).

[1] We generally judge of the distance of a source of sound only by the quality of intensity; hence, the well-known acoustic illusion employed in theatres.

With regard to these statements controversies have arisen:—the disturbance of equilibrium does not, according to Böttcher, occur in frogs after complete destruction of the labyrinth; it does occur, according to Löwenberg, after removal of the brain, and is dependent on reflex actions, which are occasioned by excitation of the labyrinth and have their centre in the thalamus.

It is supposed by Goltz, that these disturbances are attributable to the loss of the power of discrimination as to the position of the head, and that this power has its seat in the membranous labyrinth and the auditory nerve, and is dependent on the circumstance, that, whatever may be the position of the head, every change in it occasions pressure of the endolymph on a new part of the membranous labyrinth. According to another theory (that of Breuer and Crum-Brown), every movement of the head in a given direction determines a relative movement of the endolymph against the wall of the membranous canal in the opposite direction, which movement is perceived by the nerve-endings in the ampullæ.

III. THE OLFACTORY ORGAN.

The peripheral terminal organs of the olfactory nerves pass as numerous branches through the foramina of the cribriform plate of the ethmoid into the cavity of the nose, and are expanded on a membrane, which, as a mucous membrane, lines the upper part of the nasal cavity, and is distinguished from the mucous membrane proper of the nose (Schneiderian membrane) by its lighter colour and the absence of the ciliary epithelium. These terminal organs are excited by certain gaseous bodies in a manner at present totally unknown, nor do we know the properties to which they owe their excitability. The odorous particles are conducted to the olfactory membrane by inspiration through the nose. The inspired current is split up at the anterior prominent ridge of the inferior turbinated bone, and a part of it, instead of passing directly along the inferior meatus to the posterior nares, takes a circuitous course along the upper parts of the nasal cavity (Bidder). The excitation, it appears, takes place only at the first moment of contact, for to ensure a more permanent sensation it is necessary that fresh particles of the exciting body should be brought continually in contact with the terminal organs, or, in other words, that the particles should pass in a current through the olfactory organ, and the effect is greater the quicker the renewal of the particles takes place, *i.e.* the more rapid the current.

The olfactory bulbs, which were formerly considered as a part of the olfactory nerves, are now more properly considered to be parts of the brain. The olfactory nerves proper are distinguished from other nerves by consisting of a number of small bundles, each of which again is composed of numerous, extremely fine primitive nerve fibres, surrounded by a common areolar membrane. The olfactory membrane which lines the two upper turbinated bones and the upper part of the septum ('regio olfactoria') has the following construction (M. Schultze): Between the cylindrical epithelial cells, pointed at their basal end, there are found bipolar spindle cells, which send one process to the surface and another into the interior; the latter is said to be identical with the delicate primitive nerve fibres of the olfactory nerve, the other process is provided with a bundle of very long tender hairlets, which project beyond the surface; the spindle-cells are thus considered to be nerve-cells. According to recent researches (Exner), the cells found in the frog, and formerly described as simple epithelial cells, are likewise nerve-cells and are provided with hairs.

That gaseous bodies only possess the power of exciting the olfactory organs is evident from the fact that the filling up of the nose with an odoriferous (volatile) fluid, such as eau-de-Cologne, produces no sensation of smell (Weber). It is well known also that the body to be smelled must pass through the olfactory region in a current, for every sensation of smell can be at once stopped by holding the breath or by inspiring exclusively through the mouth, even if the atmosphere, and therefore also the air in the nasal cavity, be filled with the odorous substance. On the other hand, rapid and repeated respirations ('sniffing') increase the impression of smell.

The necessity of the conveyance of the current to the olfactory region by the anterior promontory of the inferior turbinated bone is seen from the fact that the odorous body is not smelled when first passed into the mouth and thence *through the* posterior nares into the nose (Bidder). Most of the odorous substances act already even when diluted to an extraordinary extent, so that an exceedingly small quantity mixed with the atmosphere of the room can readily be perceived. Recently it has been shown that most of the odorous vapours possess a large capacity for absorbing heat (Tyndall).

The Sensations of Smell.

Excitation of the terminal olfactory organs, possibly also an excitation of any kind of the nerve trunks themselves, gives rise to certain sensations, which we call odours. They are distinguished both as regards their intensity and character. The intensity seems to depend—1. On the quantity of odorous body in the gaseous mixture. 2. On the velocity of the current passing through the olfactory region. 3. On the number of excited olfactory elements. It appears at least that those animals possess the most delicate perception of smell, whose olfactory organs cover a large surface. The cause of the special

character of an odour is totally unknown, and we possess no
division nor scale, nor even a name for the different odours, but
call them only after the body to which they belong, and of
which the same or similar character of the smell reminds us.

It is scarcely doubtful, after the analogy of all the other sense organs,
that mechanical, electrical, &c. irritation of the olfactory nerve produces
the sensation of smell; experimentally, this has, however, as yet, not been
proved. The only sure way to direct electric currents to the olfactory
nerves would consist in filling the nasal cavity with water, into which one
of the two electrodes is inserted, but here the simultaneous irritation of
the sensible fibres of the trigeminus produces such violent pain, that we can-
not decide as to the sensations of smell produced at the same time (Rosen-
thal). In the excitation of the terminal organs of the olfactory nerve by
odorous substances, the hairs on the cells above described seem to take an
important part; this seems probable from the fact that by filling the nasal
cavity with water [1] the sense of smell disappears for a short time (E. H.
Weber); some have also observed that by the contact of these hairs with
water they swell up and are invisible for some time (Schultze).

The principle of specific energies (p. 343) would justify us in assuming
here also, the same as has been shown for the organs of sight and
hearing (pp. 391 and 441), the existence of different olfactory fibres, each of
which would be excited by a particular kind of olfactory stimulus and give
rise to a particular sensation ; we possess at present no clue whatever as to
how many such fibres are likely to exist.

From the olfactory sensations proper we have to distinguish those
impressions which depend on the irritation of the sensory fibres of the fifth
nerve present in the nasal mucous membrane; thus ammoniacal vapour acts
on the latter chiefly, and is therefore still perceived as a sensation after
the olfactory terminations have been destroyed, or it may cause reflex actions
(sneezing).

We know very little about subjective sensations of smell; in certain
pathological conditions of the nose (catarrh, &c.), the sense of smell is for
a time quite suspended, or even replaced by abnormal sensations of smell.

About ' after-smells ' we know next to nothing. The author observes that
for several hours after experiencing certain strong odours, such as cadaverous
odours, every unpleasant smell has, with him, most distinctly, the character
of the first.

As regards the relations of the two nasal cavities to each other, we only
know that the simultaneous irritation of the two by different odours does
not give rise to one impression, but causes a sort of race between the two
(Valentin).

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[1] In filling the nasal cavity with fluids, these are poured in through the nares,
the body taking up the recumbent posture, resting on the back. The fluid is pre-
vented from running out through the posterior nares by the velum palati, which
adapts itself to the wall of the pharynx.

The nasal mucous membrane may be considered to act as a protecting organ to the olfactory region, by liberating the traversing air from its coarser noxious admixtures. On the other hand, the olfactory organ may be considered as keeping guard for the respiration, inasmuch as many of the noxious impurities of the atmosphere affect the sense of smell.

IV. THE ORGAN OF TASTE.

Our knowledge of the sense of taste is more fragmentary than that of any other sense organ. The seat of this sense has not even been accurately fixed, and for the following reasons:— 1. Because it is difficult to separate this sensation from other sensations which are evoked at the same time on the application of the substance to be tasted, namely odorous and tactile sensations. 2. Because fluids which possess a taste pass so easily from any one spot of the mouth, and therefore possibly from a spot not endowed with taste to the proper taste organs. The special seat of the gustatory sensibility has therefore been very differently stated. Undoubtedly the root of the tongue plays an important part, but it is doubtful whether it alone (Bidder, Wagner), or also the tip and the borders of the tongue (Schirmer, Klaatsch and Stich, Camerer), the soft palate (J. Müller, Drielsma), or at least a part of it (Schirmer, Klaatsch and Stich), or even the hard palate (Drielsma), are seats of gustatory sensation. Researches with limited electric irritation (Neumann) show the tip of the tongue and its borders over an area of several lines to be capable of appreciating taste, though not all qualities of taste (Lussana); the anterior part of the upper surface, the whole of the lower surface, and the frænum are devoid of gustatory sensitiveness.

The *nerves* presiding over taste seem to belong to several cranial nerves. Besides the glosso-pharyngeal nerve, about whose function there can be no doubt, the lingual branch of the fifth is considered by many to be a nerve of taste, though some observers believe that it derives its gustatory fibres from the chorda tympani branch of the facial nerve ; the rami palatini of the fifth are likewise considered to be gustatory.

In facial palsy disturbances of taste are very common. Against the participation of the facial nerve it is asserted that after section of the chorda

tympani, no degenerated nerve fibres are to be found in the lingual nerve beyond the point of departure of the salivary nerves (Vulpian); others, however, have found such degenerated nerve-fibres (Prevost) (in the dog even, Vulpian). Since a case has been recorded, in which the intra-cranial portion of the facial nerve was found totally degenerated, without there having been any disturbance of taste (Wachsmuth), it is now assumed that the gustatory fibres join the facial nerve only by the N. petrosus super-ficialis major and enter the course of the trigeminus partly by the N. petrosus superficialis minor and the otic ganglion, and partly by the chorda tympani (Schiff). Since we may have paralysis of the fifth without dis-turbances of taste, it is quite possible that fibres of the glosso-pharyngeal nerve pass by means of Jacobson's anastomosis (N. petrosus superficialis minor and the otic ganglion) into the fifth.

The terminal organs of the nerves of taste are found in the papillæ of the tongue. The furrow surrounding the circum-vallate papillæ at the root of the tongue dips down, and forms a capillary space, the inner side of which is provided with the terminal organs of the gustatory nerves, while the free surface of the papillæ shows the ordinary structure of the mucous membrane of the tongue; these terminal organs are the *gusta-tory bulbs*, or 'gustatory goblets,' and consist of goblet-like organs, open externally, and filled with cells; of the cells themselves those more centrally situated, 'the gustatory cells proper,' terminate peripherically in a short rod, while their central ends pass into fine nerve fibres, which, in the interior of the papillæ, are connected with medullary nerve fibres (Lovén, Schwalbe). The fluid to be tasted must therefore first enter the capillary space mentioned. These spaces containing the gustatory bodies are found also in the form of plane surfaces in the *papillæ foliatæ* of man, and most animals (generally there is one at each border of the posterior part of the tongue, while in man it consists again of five parallel longitudinal rows; C. Mayer, Krause, and v. Wyss). The fungi-form papillæ possess gustatory bodies on their upper surface (Lovén), and, according to some, the free surface of the papillæ circumvallatæ is also provided with them (Schwalbe, Hönig-schmied).

The gustatory nerves are excited by certain substances which are fluid, or at least soluble in the fluids secreted in the oral cavity; probably also most (Stich) gases which possess any taste belong to this class. The process of excitation is totally unknown. 'Gustatory sensations' are the results of the excita-

tion of the terminal organs as well as of the trunks of the gustatory nerves themselves, and these are distinguished both as to their intensity and character. The intensity of the sensation depends on the force and duration of the excitation, and the number of excited nerve fibres. If the excitation be, therefore, caused by a sapid substance, then the taste will be the more intense—1, the more sapid the substance is ; 2, the more concentrated it is ; 3, the longer it acts ; 4, the larger the surface of the taste organ it is in contact with ; 5, the more easily excited the nerve fibre. The properties are not known by means of which the tasting substance produces the different empirical and undefinable characters of taste which are known, such as sweet, bitter, acid, alkaline, salty, putrid ; the different sweet-tasting bodies (*e.g.* the different kinds of sugar, glycerin, glycine, salts of lead, beryll-salts, etc.) belong to the most varied groups, and show no relations in their other properties.

As regards the taste of substances of the different chemical groups, the following facts may be noticed : the sour taste of the soluble acids ; the sweet taste of all polyatomic alcohols, which contain as many OH- groups as they contain C atoms (to this group belong $C_2H_4(OH)_2$ Glycol. ; $C_3H_5(OH)_3$ Glycerin ; $C_4H_6(OH)_4$ Lichen-sugar ; $C_6H_8(OH)_6$ Mannite [less 2 H grape sugar] ; the bitter taste of many compound sugars (glucosides), many alkaloids, etc.

In man the excitation of the trunks of the gustatory nerves can only be effected by electricity. If an ascending current be passed through the gustatory nerves (as by putting the positive electrode to the tip of the tongue, the negative electrode being in contact with any other part of the body, say the hand), a distinctly acid taste is perceived : if the current is a descending one, the taste becomes burning and 'alkaline.' If now, in this case, we had a direct excitation of the nerves by the current, the production of different tastes, according to the direction of the current, would speak against the principle of specific energies (p. 344). It has, therefore, been attempted to explain the results as due to the tasting of the electrolytic products separated out on the tongue. The observation that the results remain the same, when the current is passed to the tongue, not by immediate metallic contact, but by the interposition of moist conductors, does not disprove this explanation, because at the boundary of two moist conductors, and especially, between nerve contents and membrane, electrolytic products are deposited.

Besides gustatory sensations, the excitation of the nerves of taste causes, in a reflex manner, secretion of the salivary glands. (See p. 94.)

We know nothing definite about subjective gustatory sensations, though their existence is demonstrated ('after-taste,' etc.). Here, too, we have to distinguish between the subjective gustatory sensations and those sensations which depend on certain conditions of the buccal mucous membrane ('perverse' tastes in catarrh, etc.).

V. THE REMAINING SENSE-ORGANS.

The perceptions produced by the other centripetal nerves (excepting the optic, auditory, olfactory, and gustatory nerves) are known as ' common sensations.' Sensory nerves are found in almost every part of the body, but not to the same extent; the intestines seem to contain the least, and the muscles, bones, fasciæ, etc. are but sparingly provided with them; most numerously, however, are they distributed over the skin and the adjoining mucous membranes (the mucous membrane of the oral and nasal cavities, the conjunctiva, etc.).

The terminations of the sensory nerves are only known for a few localities, and their minute structure is, as yet, the subject of much contention. The following forms have hitherto been described :—1. Pacinian (Vater's) corpuscules; they are relatively large (0.5—4^{mm}), and are situated in the subcutaneous cellular tissue, especially of the hollow of the hand and foot; they are also found in the genital organs, many muscles and joints, and in the sympathic plexus of the abdomen (for instance, in the mesentery of the cat). They are egg-shaped, and consist of many concentric lamellæ of areolar tissue, enclosing a cylindrical body, consisting of protoplasm (inner bulb); into this the nerve-fibre enters, runs along its interior as a simple axis-cylinder, and terminates, often after splitting up into several branches, in a button-like swelling extremity. The nerve-fibre, before it enters the corpuscule, is surrounded by a *lamellated* neurilemma. 2. Terminal nerve bodies (Krause's corpuscules) are oval, or more or less rounded vesicles of 0.03—0.06^{mm}, consisting of an areolar sheath, with nuclei and soft homogeneous contents, in which the nerve-fibre runs, terminating in a point; they are found in many organs, especially in the mucous membranes, where they occupy the areolar mucosa. Possibly the organs mentioned under 1 and 2 are mere modifications of the same form of which the last-mentioned most likely presents the primary type. 3. '*Tactile corpuscules*' (Wagner and Meissner). They are found in some of the papillæ of the cutis (the rest of the papillæ contain capillary hoops), more particularly in the hollow of the hand and sole of the foot; they form elongated, oval clubs, coarsely and irregularly striated, 0.05—0.1^{mm} long, which take up nearly the whole papilla, and into which one or two nerve-fibres or parts of a nerve-fibre enter; the mode of termination of the entering nerve is, as yet, doubtful; some believe that they split up into branches and that each branch is again broken up into small transverse branchlets, which are

the cause of the transverse striation; a more recent view, however, is that the tactile corpuscule consists only of a nerve-tube assuming the form of a skein; such 'terminal nerve bundles' are seen distinctly and well developed in the glans penis (Tomsa). In the interior of the corpuscule, the branches of the nerve-fibres are said to terminate in a manner similar to that observed in the Pacinian body (Grandry). 4. *' Terminal nerve-buds.'* The terminations of the sensory nerves of the cornea. Here the nerves break up into fine branches, which form a network in the subepithelial layer, and thence send filaments, sometimes branched again, into the epithelium, and which terminate on the free surface, floating in the lacrymal fluid (Cohnheim); according to others, these filaments terminate when yet within the epithelium in a small knob (Hoyer). A similar mode of termination seems to hold good for the sensory cutaneous nerves (Langerhans, Podcopaew, Eberth). The mode of termination of the sensory (and reflex) nerves, in many places, is as yet unknown. Ganglionic bodies are observed in the skin which may possibly be terminal organs of sensory nerves (Tomsa). There are, also, special terminal organs, some of which are connected with tactile hairs, as, for instance, in the web of the bat, ear of the mouse, snout of mole, etc.

Qualities of the Sensations under consideration.

Any intense excitation of the nerves under consideration, which are distinguished as the ' sensory nerves ' in the limited sense of the word, from the preceding nerves of special sensibility, is felt as an unpleasant sensation, as *pain*, whether the terminal organs or the trunks of the nerves be excited. A large portion of these nerves, namely, those supplying the intestines, the bones, the vessels, etc., seem excitable only by ' pathological ' agencies, and then always to cause pain, if their function be not to call forth reflex actions. The rest, however, give rise, when their end organs are normally and not so strongly excited, to various sensations. The excitation of the end-organs may be brought about by very different processes, by chemical, mechanical, and thermal agents, but not by the vibrations of light and sound. This harmony of the specific excitants (p. 344) with the general nerve irritants, favours the idea that the end organs of the sensory nerves are of simple construction, and not very different from the nerve trunks, and perhaps only made more accessible to the exciting processes of the external world by their position. The sensations which are produced by mechanical irritation of the end-organs are called *Tactile sensations :* those which follow thermic irritation, *Sensations of temperature.*

Recent observations have made it very doubtful, whether painful irritations of the skin are merely due to a stronger irritation of the ordinary nerve terminations, or whether rather to an irritation of special end organs. For there seem, according to some observers, to be different roads of conduction in the brain, both for tactile sensations and painful sensations, such, for instance, as are caused by chemical irritation of the skin (tactile and pathic channels, see Chap. XI.); it is possible, therefore, that in these two cases, different peripheral apparatus may be concerned, and it has, moreover, already been stated that the modes of termination of the nerves in the skin are various.

The following experiment (E. H. Weber) proves that sensations of temperature can only be caused by the thermic irritation of the *end-organs.* If the elbow is dipped into a very cold fluid, the cold is only felt at the immersed part of the body (where the fibres terminate); pain, however, is felt in the terminal organs of the ulnar nerve, namely, in the finger-points; this pain, at the same time, deafens the local sensation of cold. This experiment serves, likewise, to prove that the cause of excitation is referred to the end organ (p. 345).

Tactile Sensations.

Tactile sensations are produced by mechanical irritation of different degrees, by contact and by pressure.

The limit at which the intensity of the irritation becomes painful is different for different parts of the body. By help of the tactile sensation we are able to come to the following conclusions :— 1. We conclude as to the existence of a foreign body touching our body. 2. From the intensity of the sensation we estimate the force of the pressure exerted, and from this we estimate, under given circumstances, the weight, tension, etc., of the touching body. The muscular sensation is an important aid in these estimations (*i.e.* the sensation of the degree of exertion in the muscles concerned in carrying, lifting, drawing, pressing (see below). 3. We have always an idea of the state of irritation of all our sensory fibres, and feel therefore our whole body surface as a 'tactile field,' similar to the field of vision (compare p. 395). We are thus enabled to determine immediately the locality of each part touched, and thus also the position of the touching body. 4. When a body touches a cutaneous surface, or several cutaneous points simultaneously, we are enabled, from the position of the different points of contact, from the different pressure, and from the spaces not touched, to draw conclusion as to the configuration of the touching body. This conclusion becomes still more positive when

we pass the skin over the touching body, and thus create for ourselves a number of tactile pictures. For this purpose those cutaneous surfaces are best fitted which possess great mobility, and contain numerous sensory end-organs, *i.e.* the finger-tips, the point of tongue (see below). If different parts of the cutaneous surface touch the same body, a knowledge of the relative position of the different cutaneous surfaces is necessary in order to determine the configuration of the touching body. This knowledge we obtain through the muscular sensation (see below), because muscular movements are necessary for nearly every change of the relative position. If this knowledge is wanting, as, for instance, in abnormally distorted displacements of position, false conceptions arise about the configuration of the body. The ' experiment of Aristotle' belongs to this class : By placing the middle finger so over the index finger that a small round body (pea, penholder) can be brought or rolled about between the radial side of the index finger and the ulnar side of the middle finger, the sensation of *two* round bodies is produced, because one body cannot be brought in contact with these two surfaces without producing distortion. By its very uniform touch we conclude the presence of a fluid, and by the more or less increasing pressure, when the tactile surface moves about, we estimate the more or less soft or hard consistency of a body, etc. These different conclusions are often enumerated as specific ' senses ' (*Sense of pressure, sense of locality*, etc.).

The perceptive power of the sensory nerves depends, as regards its sensitiveness for each part of the body, on the following : 1. On the richer or poorer distribution of its end organs. 2. On the absolute sensitiveness of the part.

The *number* of end organs in the different cutaneous surfaces can only be determined anatomically ; experimentally, however, we can get relative data as to their distribution ; the method is the following (E. H. Weber, Czermak) : 1. Find the smallest distance which can intervene between two bodies touching the skin, either simultaneously or shortly after one another, in order to produce two separate sensations ; the instrument used consists in a pair of compasses with blunt points, which can be placed on the skin at different, easily read off, distances (the eyes being shut). The distance is found to be smallest on the tip of the tongue ($1\cdot1^{mm}$), on the palmar side of the third

phalanx ($2 \cdot 2^{mm}$), and the red surface of the lips ($4 \cdot 4^{mm}$); largest on back, chest, neck, and extremities ($35 — 66^{mm}$).

The smallest required distance is in some places, for instance on the extremities, less in the transverse than in the longitudinal direction; it is less also when the points are placed on the skin one *after* the other; it is less, by beginning with larger distances and gradually finding that distance at which both impressions blend, than proceeding in the reverse order, and beginning at a smaller distance and gradually finding that distance at which the two separate sensations make their appearance ; lastly, it becomes smaller the greater the attention and the greater the practice (hence it is generally smaller in blind people, Goltz) ; it is also said to become smaller by surrounding the skin with indifferent fluids (oil, water), having the same temperature as the body (Suslowa). Two impressions just felt distinct from each other blend into one when the skin between the two touched points is irritated by tickling or induction currents (Suslowa); for the explanation of this see below. 2. Move the two separately felt points of the compass over the skin in two parallel lines, keeping the same distance, and determine the variations in the apparent distance and the distance at which the two separate sensations blend. 3. The eyes being closed at the time, touch a point of the skin, and note accurately the apparent place of touch.

The absolute *sensitiveness* of any cutaneous part is determined in the following way :—1. Two different weights are placed on a cutaneous part, and the smallest difference in weight which can yet be perceived is accurately determined. The loading is done either by weights placed unsupported on the part (Weber), or by *loaded* small plates (Aubert and Kammler), or by a blunted point suspended on one beam of a balance, the weight of the point being taken off, *equalized,* in different degrees, by weights attached to the other beam of the balance (Dohrn). Here also the sensibility is found to be more delicate with the increase than the decrease of the difference in the weights, and also with a smaller absolute pressure than with a larger. 2. By determining the smallest possible *variation in pressure* which a cutaneous part can perceive (Goltz); an india-rubber tube, filled with water, and to ensure a constant surface of contact, bent at one spot

over a piece of cork, is touched at that spot by the cutaneous part to be examined, and by rhythmically exerted pressure, waves, analogous to those of the arterial pulse, are produced in the tube. This method gives the same scale of results as Weber's experiment with the compasses; the tip of the tongue only forms a remarkable exception, inasmuch as its sensation for pressure stands much lower than in the other scale for measuring the sense of locality. 3. The smallest possible irritation which can yet be felt is determined; it has thus been found that an impression or touch which can just be felt, ceases to be so on passing weak unfelt induction currents through the cutaneous part touched (Suslowa.)

Of the last-mentioned three methods the second is the most decisive, for we are naturally only sensitive to *variations in pressure*, and these take place in the second method with greater rapidity and precision than in the first. It is, however, to be observed, that in the second mode of experimentation the *sense of space* is not altogether excluded, for with the positive variation of pressure there is, most likely, also, a slight increase in the surfaces of contact, as both the tube and the cutaneous part are mutually flattened, and experience teaches us that we are able to feel the arterial pulsations in many places, whilst the cutaneous part touched does not perceive it, though the same variation of pressure acts on it too. Already, comparisons of this kind may be used for the construction of a scale (Goltz). The third method becomes most reliable by using an electromagnetic motor apparatus to produce irritation (Leyden); the results thus obtained are, however, only to be used with caution, on account of the different resistances in the conductivity of the mucous membranes and the epidermis of different parts of the cutaneous surface.

Lastly, there are methods for determining at the same time the sensibility of the cutaneous parts in both directions, namely, by finding the degree of perfection of our conclusions as to the configuration or the course of touching bodies. 1. The skin is touched with bodies of a definite configuration. 2. Different figures (letters) are drawn on the skin with a point, and one now states in the first case the apparent figure of the body, and in the second that of the drawing.

In order to explain the above-stated facts about the separation in space of the tactile impressions, the following assumptions are necesssary (Lotze, E. H. Weber, Meissner, Czermak). We are continually conscious of the state of irritation of all the cutaneous points in their given arrangement in space (our consciousness perceives a field of tactile sensation, as already stated).

Every irritation of a sensory end-organ is referred to a definite spot in the field of tactile sensibility, that is, on the surface of the skin. This spot is, however, not the *point* irritated, but rather a circular or (on the extremities, p. 461) an oval *plane*, the centre of which is formed by the irritated point, the so-called *circle of sensibility* (see below). Two such circles, which either touch or partly cover each other, can, however, not be separately perceived; the separation takes place then only when between the two circles there is a *non-irritated sensory element* and the apparent distance of the two irritations is the greater *the more* numerous the non-irritated elements which remain between the two circles. From this it follows that two neighbouring impressions on the skin can only then be felt separate when their distance is greater than the whole diameter of one circle of sensibility. The numbers given on page 461 are therefore the diameters of the circles of sensibility at the corresponding cutaneous places. It follows further, that two separate impressions blend when the intervening sensory elements are irritated (compare the observation on p. 461).

There still remains to be explained how it is that these circles possess different sizes at the different parts of the skin. A circle of sensation is evidently not an anatomical magnitude, such as the district of distribution of a nerve-fibre, for, firstly: it is altered by attention, practice and other influences; and, secondly, it would be possible for the two feet of the compasses, if their distance were smaller than the diameter of one circle of sensation, in one case, both to fall within one circle, in another case into two neighbouring circles (these being considered fixed). We must therefore assume the existence of a circle of sensation round each cutaneous point. To the above explanation is further to be added, that the circles are the smaller the more closely packed the sensory organs (compare 461); from which it follows that the assumption, that the circle of sensation is caused by the mechanical effect of the irritation on a cutaneous surface, and not on a mere point (*circles of diffusion*), is not enough: for if so, then the size of the circles would evidently be independent of the relative number of the end-organs, and therefore would in general be the same everywhere. It is rather to be assumed, that the transmission of the irritation of one fibre to another sensory

fibre in the neighbourhood is a central process (irradiation, associated sensation), and that it always extends from every point, in every direction, to the same number of sensory fibres (the distance of the two points of the compasses corresponds in the mean to twelve tactile corpuscules, Krause), but that by practice, attention, and acuteness of irritation, etc. it can be diminished. This view (see Chap. XI., under Spinal Cord) seems to correspond best with the observed facts.

Alterations in the normal amount of blood in the skin (hyperæmia, anæmia) diminish the tactile power (Alsberg); intense cooling of the skin (for instance, ether-spray) may produce complete anæsthesia; certain poisons brought in contact with the skin act in the same way.

Sensations of Temperature.

Sensations of temperature are produced when the end-organs of sensory nerves are irritated by variations of temperature within the limits of about $+10°$ to $+47°$ C., particularly when the skin is either warmed or cooled by bodies in contact with it. The sensation caused by a positive variation we call sensation of warmth, that caused by the negative variation, sensation of cold. When the variation of temperature extends over a large surface, or over the whole body, then the sensation of cold changes to a sensation of shivering, and the sensation of warmth gives rise to a sense of heat. The symptoms mentioned at page 232 are connected with both (the shivering of fever is caused by the sudden cooling of the skin in consequence of the diminished flow of blood through the spasmodically contracted cutaneous arteries, whilst fever heat is due to the reverse process; in both, however, the mean bodily temperature is higher than normal). Variations of temperature between $27°$ and $33°$ C. are distinguished most acutely, then variations between $33° - 39°$ C. and then variations between $14° - 27°$ C. (Nothnagel). The different regions of the body may be grouped as regards their sensitiveness to changes of temperature (measured by the smallest yet perceptible variation) as follows (leaving out the extremities, which follow no law), (E. H. Weber): Tip of tongue, eyelids, cheeks, lips, neck, trunk. As the middle line is approached the parts are less sensitive. The variation is felt more intensely the more rapid its occurrence, and the larger the affected cutaneous surfaces. Temperatures above or below

the limit given above produce pain (p. 458). Variations are here no longer specifically felt.

Anæmia of the skin increases the sensitiveness for temperature; hyperæmia diminishes it (Alsberg).

If the principle of specific energies (compare p. 344) is to be a general one, we must assume here, also, different fibres and different central organs for the tactile and temperature sensations; though we know nothing definite about this, it may be yet mentioned that the distances in the experiment cited on p. 461 are smaller when the temperature of the two points of the compasses differ (Czermak), and that in the experiments given on p. 461 a colder weight is felt as heavier, so that the apparent difference of pressure becomes greater when the heavier weight is at the same time colder, and less when the lighter weight is colder, and that difference of pressure is felt with equal weights of unequal temperature (Weber).

Other Specific Sensations.

The sensory nerves of certain parts of the skin and mucous membrane of the genital organs (4th section), on being irritated, give rise to peculiar sensations, different from the tactile and temperature sensations, which are called *voluptuous sensations.*

We know very little about the specific sensations of those nerve-fibres which do not terminate in the skin. Some of these sensations, *hunger* and *thirst,* have already been considered (p. 197). There only remain for consideration—

The *muscular* sense (Weber). The presence of sensory fibres, though not anatomically demonstrated with certainty, is physiologically proved by the muscular pains observed under certain conditions, and by the *sense of fatigue* which undoubtedly exists. The question is only whether these or other nerve-fibres explain to us the *state of activity* of the muscles. It is evident that many phenomena, such for instance as the combination of complicated muscular movements, depend on the intervention of centripetal fibres, for such movements become very defective when the posterior roots of the spinal nerves are divided (Bernard), or when the centripetally conducting parts of the spinal cord (see Chap. XI.) are injured or degenerated (for instance, in the gray degeneration of the posterior columns (locomotor ataxy). It is very improbable that these defects depend on the loss of cutaneous sensibility, for the movements are not at all or very little interfered with by skinning the animal (Bernard). It seems therefore that con-

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sciousness itself is aware of the condition of the muscles, etc. This may be brought about in the following ways. 1. Sensory nerves of the muscles give information about the changes in tension, pressure, and possibly also of the state of contraction. 2. Our consciousness judges of the voluntary impulse, which is imparted to the motor nerves, and of the effects which necessarily follow. 3. The sensorium is made aware of the effects of muscular activity by the surrounding parts (muscles, areolar tissue, etc.). Whether all these different ways or one of them only exists, is not known. The various uses of such a muscular sense are evident, partly from what has just been said—estimation of weights lifted, knowledge as to the configuration of the surface of, and conclusions as to the form of bodies touching.

In the joints, periosteum, and more rarely in muscles, Pacinian bodies (p. 457) have been found, which perhaps have some relation to the muscular sense (sub 3 in the above paragraph), (Rauber.)

CHAPTER XI.

THE CENTRAL END-ORGANS OF NERVES. (CENTRAL NERVOUS ORGANS.)

A. GENERAL CONSIDERATIONS.

THE central end-organs of nerve-fibres are contained in certain structures, which are called the ' central organs of the nervous system.' The latter contain, in addition to the central end-organs, numerous conducting fibres. Their function is, therefore, much complicated by the fact that they are able to act also as conducting agents. Since the investigation of the central nervous end-organs has never, hitherto, been possible apart from the nerve-fibres with which they are mixed, a physiological consideration of them is not possible in the present state of our knowledge. We can, therefore, only give the discoveries which have been made concerning the functions of the mixed organs—brain, spinal cord, and ganglia—to serve as material for the future physiology of the nervous end-organs which have not yet been isolated.

The characteristics which go to constitute a central nervous organ are, according to what was said in the introduction, the following :—1. The liberation of the active condition in a ('centrifugal') nerve-fibre, without the apparent participation of any external influence—*automatism*. 2. The liberation of the active condition in one ('centrifugal') nerve-fibre, brought about through another ('centripetal') fibre—*reflex action*. 3. The phenomena collectively called *states of consciousness* or *mental operations*, which are connected with the irritation of certain central organs.

All organs of the body which can be shown to possess the above characteristics contain as necessary constituents *ganglion-*

cells, which are immediately in communication with nerve-fibres. Since no other structures, with the exception of the peripheral end-organs previously mentioned, are known to be in undoubted continuation with nerve-fibres, these ganglion-cells must, in general, be regarded as the central end-organs of nerve-fibres. It is, nevertheless, still doubtful (1) whether all ganglion-cells ought to be considered as central organs, and (2) whether there do not exist other central organs in addition to ganglion-cells.

The former of these doubtful points seems to be settled in the negative by the expression, in general use, of 'peripheral ganglion-cells.' That is to say, in many organs, the functions of which are certainly not those of central nervous organs, nerve-fibres are found to be provided with ganglion-cells or cellular apparatus much resembling them. This is seen to be the case in the organs of sense, in glands, &c. If, however, the power of transferring a stimulus from one nerve-fibre to another be regarded as a general character-istic of a central organ, it is quite possible to look upon the 'peripheral ganglion-cells,' the exact signification of which is yet entirely unknown, as also belonging to the class of nervous central organs. Every fibre in the course of which is interposed a ganglion-cell must, accordingly, be regarded as a system of two fibres, of which one is provided with a peripheral end-organ, while the other, like the numerous intercentral fibres of brain, spinal cord, and sympathetic nervous system, connects together two central organs. With respect to the second question, as to the use of ganglion-cells only as central organs, it may be stated that there exist in the brain numberless small cellular organs of manifold form, which have been distin-guished from ganglion-cells, but whose nature appears essentially to agree with that of the latter bodies to the extent that it is in general nervous.

Many anatomical peculiarities in the structure of the central organs can only be made out in preparations in which, besides the changes accompany-ing the death of the tissues, certain others, of the nature of coagulation, &c., have been induced by means of reagents. Very little is therefore known of the real structures of the organs during life.

Properties of Ganglion-Cells.

Of the properties of ganglion-cells almost nothing is known. The nature of their chemical composition can only be imperfectly and approximately gathered from analyses of the grey substance of the brain. The white substance of the brain, which consists essentially of nerve-fibres and a connecting substance (neuroglia), is considered to be of the same composition as nerve-trunks; the constituents of the latter indeed have been chiefly deter-mined by examinations of brain and spinal cord. While the

reaction to test-paper of the white substance is neutral or alkaline, the grey substance has been found to be acid (Gscheidlen),—a circumstance which is probably to be attributed to the rapid changes occurring at the surface of section. The chemical constituents of the white substance are lecithin, protagon, and probably other lecithin-bodies; albumin, potassium-albuminate and globulins; cholesterin and fats; creatine, xanthine, and hypoxanthine; inosite and some anhydride of sugar; lactic acid (the ordinary modification according to Gscheidlen) and volatile fatty acids; salts and water. The grey substance of the brain is distinguished chemically from the white chiefly by containing more water, albumin, lecithin, and lactic acid, and less cholesterin, fat and protagon.

A considerable number of substances which are now known to be either the products of the decomposition of lecithin, or the mixtures of such products with other bodies, were formerly described as genuine constituents of brain substance. Even the above-mentioned constituents may be themselves the results of the decomposition of more complicated pre-existing compounds. One of them, protagon, has recently been regarded as a mixture of lecithine and a nitrogenous glucoside, cerebrin (Hoppe-Seyler), a body which chiefly occurs in the white substance (Petrowsky). The composition of grey and white brain-substance is given in the following Table (Petrowsky):

	Grey substance.	White substance.
Water	81·6 p.c.	68·4 p.c.
Solids	18·4	31·6
Consisting of		
Albumins and gelatin . .	55·4 p.c.	24·7 p.c.
Lecithine	17·2	9·9
Cholesterin and fats . .	18·7	51·9
Cerebrine	0·5	9·5
Substances insoluble in ether .	6·7	3·3
Salts	1·5	0·6

It is in the highest degree probable that processes of oxidation take place in ganglion-cells as in all other organs. It is, however, still but a probability, unless we consider it evidenced by the fact that the venous blood of the brain and spinal cord is as poor in oxygen and as rich in carbonic acid (*i.e.* as dark in colour), as the venous blood of any other region of the body. We are equally ignorant as to whether such processes of oxidation are concerned in the activity of the ganglion-cells, and, if so, to what extent; we cannot say whether that activity is not de-

pendent upon processes of decomposition similar to those which occur in muscles and nerves; or what the results of such oxidations or decompositions are.

Still less is known of the transformation of energy in ganglion-cells. As far as can be judged the energies which become kinetic or free in ganglion-cells are not of a nature which admits of investigation by the means at our disposal. We must suppose in general that molecular processes occur in them similar to, and immediately connected with, those which are assumed to occur in nerve-fibres (p. 342). If the active condition of a nerve-fibre be imagined as a chain of successive liberations of force, the manifestation of energy in the ganglion-cell must be regarded as the initial or final link of that chain; and the question now arises: What, in the first place, is the force which liberates the potential energy of the ganglion-cell, and what, in the second, becomes of the force thus set free?

The answer to these questions seems to be simplest in the case where the cell is intermediate between two nerve-fibres, *i.e.* in the case of *reflex* activities in the widest sense of the term. Here the potential energy of the ganglion-cell is set free by means of the energy, already liberated, of the stimulated fibre; and the energy thus become kinetic, in its turn sets free the energy which is potential in the second fibre. In this case, therefore, we have but a single chain of liberations, the initial link of which (the original liberating force) is some influence in the external medium, which operates upon a peripheral end-organ (organ of sense); and the final link of which is the liberation of the potential energy of some organ of work such as a muscle, a gland, or a parenchyma. The ganglion-cell, in such a case, performs a function which differs in no essential respect from that of any portion of a simple conducting fibre.

But the process which takes place during stimulations which are characterized as *automatic* is far more difficult to understand. Under the title of automatic are included all those stimulations proceeding from a ganglion-cell in which the liberating force in the ganglion-cell is unknown. In this case two possible theories present themselves. Either the liberation of energy within the cell takes place without the aid of any liberating force, or the automatism is only apparent, the liberation being due to some operation of a reflex nature. Possibly

many apparently automatic stimulations are to be explained on the latter supposition, as, indeed, has already been the case with some, viz. with the liberation of the respiratory movements (p. 168); with muscular tonus, &c.

In the former case, in which energy is supposed to be set free without the aid of any liberating force, it would be necessary to assume a continuous liberation of energy.[1] The stimulation of the nerve-fibre brought about by it need not, however, be continuous. Suppose, for instance, that the energy liberated has to overcome a certain resistance before being able to act as a stimulus upon the nerve-fibre, it would then be necessary for the tension of the energy liberated to reach a certain amount previous to stimulation, just as gas constantly passed through a bent tube under water does not rise in the tube in a continuous stream, but in an intermittent manner in bubbles of a certain size, since it is necessary to accumulate a certain pressure in the tube in order to overcome the resistance due to the cohesion and weight of the water. In this manner a *rhythmical* stimulation is accomplished. As a fact, all stimulations, which have been shown to be automatic, are either continuous ('tonic') or rhythmical; but here it is necessary to remind the reader of the probability that even tonic stimulations ought in truth to be regarded as rhythmical (tetanic, p. 260). Any force which could increase or diminish this hypothetical resistance would influence the frequency of the rhythm and the strength of each stimulus, just as, in the above illustration, an increase in the cohesiveness of the water brought about by means of gum, &c. would render the bubbles less frequent but greater, while a diminution, brought about by using ether instead of water, would cause the bubbles to become more frequent but smaller. If the resistance were made exceedingly great, the stimuli would be discharged at long intervals, while if it were much reduced the intervals would be so slight as to render the stimulation tonic (tetanic). An influ-

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[1] Such a continuous liberation may be supposed to be caused by a continual bringing together of energy-yielding materials, effected by extraneous means (*e.g.* by the blood), in exactly the quantities in which they combine : or by the energy liberated at any one moment so acting during the next upon the stored-up potential energy as to perform the part of a liberating force, somewhat as the heat formed during the burning of tinder by a spark first serves to maintain the combustion.

ence of this kind appears, in fact, to be exerted in the case of certain ganglion-cells characterized by a rhythmico-automatic action, by means of the so-called 'regulating' nerves, of which the 'inhibitory' nerves form one class.

Certain phenomena, especially the action of some fibres of the vagus on the heart, and others upon the medulla oblongata (pp. 73 and 352), can only be explained in a very forced manner by other theories. If it be established as a certainty that the influence of those fibres upon the central organs merely consists in a modifying action exerted by them upon the organs in question, of such a nature that the activities of the latter are differently distributed as to time, and hence that the strength of every discharge of energy is inversely proportional to its frequency (p. 168), it can only be explained by assuming that the hypothetical resistance is increased by the activity of certain fibres (inhibitory fibres) and diminished by the activity of others (accelerating fibres). It is just as easy, however, to imagine that accelerating and inhibitory nerves act, the former by accelerating, and the latter by hindering, the chemical processes which occur in the central organ, the resistance meantime remaining constant. Such a theory would imply that the sum total of the magnitudes of the discharges did not remain constant, but varied,—which is indeed the case during the inhibition of the heart by the vagus (Ludwig and Coats).

We understand nothing whatever of the processes of stimulation in ganglion-cells, in which the initial or the final link in the chain of liberations is a *state of consciousness* (Will, Sensation); or of those mental operations which are not apparently directly dependent upon the stimulations of the conducting organs (Processes of Thought). It is exceedingly doubtful whether any such mental operations occur which are not connected with irritation of nerves, and therefore with sensation or will.

A theory, which, although incapable of demonstration, has been put forward in a modified form from other quarters, seems not improbable. According to it, every mental operation forms an unbroken series—a 'chain of thought'—the initial act of which has connected with it a stimulation of nerve (Sensation), and the final act of which is, in its turn, accompanied by a

state of consciousness (Will) which is also connected with nervous stimulation. It is now but a step further to suppose that an uninterrupted series or chain of successive liberations, coincident with, and in some unknown way connected with the above-mentioned series of mental operations, takes place in the central nervous organ, uniting the initial and final nervous stimulations concerned in Sensation and Will. With this hypothesis the difficulty would be removed of seeking in the central organ the beginning or end of an irregular and discontinuous process of liberation; for, according to it, the essential operations occurring in the central organs, and concerned in the phenomena of mind, would be distinguished from simple reflex acts only by the greater amount of time and space rendered necessary by the greater number of centres (organs of the mind), whose stimulation is concerned in any mental operation. Consequently, the origin of every excitation of nerve which is not automatic would have to be sought for, immediately or mediately, in the stimulation of a peripheral nervous end-organ.

This is not the place to mention the numerous philosophical views concerning the dependence of the functions of mind upon material processes, or, as it is here put, upon the forces liberated in a central organ. It must be kept in mind that the hypothesis just brought forward has nothing whatever to do with that question.

The properties which, according to what has been said above, can be ascribed on hypothetical grounds to ganglion-cells (with some reservations), are, therefore, the following: 1. A continual liberation of forces, which, in their turn, act as liberators upon the different nerve-fibres, either (*a*) without any further interruption (true tonic automatism, if such exist): or (*b*) after overcoming a certain hypothetical resistance (rhythmical and tetanic—apparently tonic—automatism), the extent of the resistance, or, according to other views, the rapidity of evolution of the force, depending in its turn upon the condition as to excitation of certain different 'regulating' fibres. 2. The power of conducting from one nerve-fibre to another, conduction taking place from a centripetal fibre, through one or more ganglion-cells, to a centrifugal fibre: if the change occurring in the ganglion-cells during conduction is not associated with states of consciousness, the process is characterized as

reflex; while, if it is so associated, the state of consciousness coincident with excitation of the central organ by means of the centripetal fibre is called Sensation, and that coincident with excitation by means of the centrifugal fibre, Will.

Whether we ought to add to the general properties of ganglion-cells that of irritability when acted on by the common nervous stimuli, is not yet decided. Certain experiments on the non-irritability of the spinal cord under mechanical stimulation, which will be discussed hereafter, indicate that ganglion-cells differ from nerves in this respect, probably to a considerable extent. The composition of the blood surrounding the cells has a most important influence upon them.

Finally, there must, most probably, be added to the general properties of ganglion-cells certain conditions of their activity as to time. 1. The number of vibrations of the 'bruit musculaire' during tetanus produced by centric stimulation (p. 260) is about 19·5 per second. Since muscle on artificial stimulation, whether directly or indirectly applied, is capable of a much quicker series of vibrations, the above number cannot be due to any property of muscle or nerve, but is most probably to be explained by supposing that the motor ganglion-cells, from which the motor nerve immediately proceeds, imparts to the nerve 19·5 impulses per second at every excitation, even when artificially induced (p. 261). 2. The excitation of the optic nerve is most intense when it takes place 17—18 times in a second (p. 387). 3. The excitation of the auditory nerve is most intense when it takes place 33 times in a second. The last two circumstances are possibly explicable on the assumption that in the sensory ganglion-cell, which is first excited by means of a centripetal fibre, every excitation takes $\frac{1}{17}$ or $\frac{1}{33}$, as the case may be, of a second to exhaust itself, in consequence of which the succeeding excitation acts with greater effect after that interval than it would if aroused earlier. The total effect, therefore, must be greatest when excitation takes place with the above-mentioned frequency.

The time taken up in conduction through the central organ (ganglion-cells, grey network) may be determined in the case of reflex actions by measuring the interval of time which elapses between stimulation and the reflex action caused by it, and subtracting therefrom the time occupied in conduction through the

sensory and motor nerves concerned, a knowledge of which may be obtained by the method given on p. 336 (Helmholtz). In this manner an interval of $\frac{1}{30}$ — $\frac{1}{10}$ of a second has been obtained, with respect to which, however, it is unknown to what extent or description of path through the central organ it refers. The time taken up by conduction through the centres is shorter the stronger the centripetal stimulation; it is, moreover, in the region of the spinal cord, greater in the case of conduction across the mesial plane, and it is increased by exhaustion of the central organs (Rosenthal).

The measurements of time, with regard to mental activities, will be given when discussing the Cerebrum.

B. SPECIAL PHYSIOLOGY OF THE CENTRAL NERVOUS ORGANS.

There must now be described whatsoever has been discovered concerning the functions, as centres and as conductors, of the various central organs, viz., brain, spinal cord, and sympathetic ganglia. It must be expressly borne in mind that only those facts which have been established with some degree of certainty will be noticed in this, the darkest, region of physiology.

1. Spinal Cord.

STRUCTURE.—The most important points, physiologically, in the structure of the spinal cord are the following:—In a cross section of the cord there are distinguished, 1. The narrow central canal lined by epithelium. 2. The grey substance which surrounds that canal, and projects in the form of horns (anterior and posterior cornua) into the white substance. 3. The white substance, in which one may distinguish on either side of the median fissures, three columns, the anterior, lateral, and posterior; between the anterior and lateral columns lies the anterior cornua of the grey substance, and the fibres of the anterior root of the spinal nerve which enter it. In like manner the posterior cornua and the fibres of the posterior root lie between the posterior and lateral columns. The white substance, besides the root fibres traversing it in an horizontal direction, consists of vertical (longitudinal) fibres and a connecting substance (neuroglia). The grey substance consists of ganglion-cells, and a homogeneous grey mass, in which the majority of recent observers describe an interlacement of fine axis cylinders running in all directions.

The ganglion-cells lie for the most part in the anterior and posterior

cornua. There is distinguished in every ganglion-cell (Deiters) a granular mass (protoplasm), a large nucleus with neucleoli and processes. Among the processes one—the axis cylinder, which, as it seems, is in connection with the nucleus—may be at once detected by its appearance; the remaining processes are fine, numerously branched, pointed fibres (processes of protoplasm), into which homogeneous fine simple fibres—axis cylinders of the second kind—are inserted. The latter join the fine network of fibres of which the main mass of the grey substance consists (Gerlach), and from which fibres, united so as to form thicker bundles, run into the white substance. According to recent theories (M. Schultze), the cells consist of a fine fibrillar network, the processes also being fibrillated (p. 322); if so, the cells are merely traversed by the fibrillæ of the processes.

The large axis cylinders (those of the first kind) are the terminations of the root-fibres of the spinal nerves. The cells into which the fibres of the anterior root enter ('motor ganglion-cells') are larger and have more numerous protoplasmic processes than the more spindle-shaped cells into which the posterior root-fibres enter ('sensory ganglion-cells'). According to another view (Gerlach), the fibres of the posterior roots do not in general enter into ganglion-cells, but pass directly into the fibrillar network of the grey substance, so that the cells of the posterior cornua also are probably to be reckoned as motor.

It is clear from the anatomical arrangement of the parts that the spinal cord is, with the exception of the thin sympathetic communications, the only connection between the brain and the nerves of the trunk and extremities. The spinal cord must therefore contain the paths for the conduction of all voluntary movements of the trunk and extremities, for all sensations in those parts, and for all actions not psychical of other cranial centra (*e.g.* the respiratory centre).

It is, however, established on anatomical grounds that the nerves of the trunk in the spinal cord do not simply run to the brain, but that all of them, or at least the motor nerves, are first of all connected with ganglion-cells. Moreover, there are physiological reasons against the view of the direct entrance of the nerves of the trunk into the brain, as will be seen on consulting the sections on Reflex Actions.

No well-ascertained anatomical facts have, as yet, been discovered which throw light on the conduction of impressions from motor and sensory ganglion-cells to the brain. It is most probable that the cells are immediately connected with a complicated network of fibres, which continues uninterruptedly to the brain, but from which fibres continually separate and run to the brain isolated in the white substance. In order to under-

stand the matter, it is necessary to assume that impressions only travel along structurally continuous paths—paths morphologically pre-existent—but that they are able to pass along those paths in every direction where continuity of the conducting structure is established. According to this supposition a nervous impression, when once it has gained the actual, anatomical network of fibres, may pass along every individual fibre which is fitted for conduction.

The result of an excitation of a sensory fibre of the trunk or extremities is either a *Sensation*, which is referred with more or less exactness to the peripheral termination of the fibre (p. 345), or a *Reflex Action*, *i.e.* an excitation of a motor fibre without the aid of consciousness, *i.e.* an excitation which is involuntary.

The production of a localised sensation implies that the excitation has been conducted in an isolated manner to the mental organs in the brain. But since all sensory fibres pass, either directly or indirectly, through a sensory ganglion-cell, into the frequently mentioned network of fibres, such an isolated conduction seems impossible. Equally unintelligible is that process which may, in a certain sense, be looked upon as the reverse of the preceding, viz. the voluntary production of isolated movements. For since the excitation of a motor ganglion-cell can apparently only be brought about by means of the grey network of fibres, which is at the same time connected with every other motor cell, it is by no means clear how excitation can be confined to the one cell concerned. In order to explain these phenomena it is necessary to have recourse to a hypothesis, which will be treated of on p. 479.

The reflex acts following excitation of the same sensory fibre may be of the most varied kinds. Individual muscles may contract, whereby regular, and, in a certain sense, purpose-like movements may be produced; or apparently disorderly movements may result, in more or less limited muscular regions, or in all the muscles of the body.

Orderly reflex movements may be best observed in animals the mental organs of which have been removed by separation of the brain from the spinal cord ; and, for the latter operation, frogs are the most convenient. Beheaded frogs when stimulated make regular and purpose-like movements of defence, which

differ so little from voluntary movements having the same object that some have ascribed them to mental organs situated in the spinal cord (Pflüger). Exactly similar reflex movements occur when the mental organs of the brain are rendered inactive during sleep; and involuntary and orderly reflex actions continually occur, even in a wakeful condition, for the purpose of escaping some form or other of stimulation applied to the body.

A beheaded, or brainless, frog will take up a sitting posture like the uninjured animal; if pinched with forceps it will press with the feet against the instrument in order to push it away; if a drop of acid be placed upon the skin, it whisks it off at once with its feet, &c. These protective movements are very regular, but they admit of variations. If, for instance, that leg be cut off which is employed under ordinary circumstances in the removal of an irritant from a certain spot of skin, another limb will be brought into play, after some ineffectual movements of the stump, for the accomplishment of the same object. In this case the stimulus is not indeed the usual one; but it has had time, during the vain attempts of the frog to remove the irritant by means of the stump, to reach such an intensity that a mechanical explanation of the phenomenon is still possible. During sleep irritation by tickling, &c. produces unconscious but orderly and purpose-like movements.

The attempt to explain these facts by assuming the existence of mental organs in the spinal cord will be discussed below.

Orderly reflex acts have not all a defensive character, many purposive reflex processes having other objects. Thus, it may be observed in frogs whose cerebra have been separated from their spinal cords (Goltz):—1. That they croak regularly when the skin in the neighbourhood of the back is gently stroked, or when the nerves supplying that skin are mechanically irritated. 2. That, during the breeding season, the male will clasp the female firmly and continuously if the back of the latter be applied to the breast of the former, or if any other similarly shaped structure, such as the finger of the experimenter, or the back of a male frog, be similarly applied. On the other hand an uninjured frog does not croak regularly on having its back stroked, and will only clasp an object as it is accustomed to clasp the female if copulation have been interrupted immediately before (Goltz). The consideration of these differences will be resumed hereafter.

For the performance of orderly reflex acts that portion of the cord with which the implicated sensory and motor nerves are directly connected is all that is necessary. For example, the second experiment above detailed may be shown with only that portion of the trunk bearing the anterior extremi-

ties, viz. with the portion of the back between the skull and the fourth vertebra, and the attached shoulder-girdle and arms.

Besides orderly reflex movements, movements of a disorderly nature, without any definite object, may occur : such movements are described as reflex convulsions. They only take place under abnormal conditions, as, for example, on very powerful stimulation, or after the operation of certain poisons (strychnia), or of certain pathological processes (traumatic and rheumatic tetanus, hydrophobia). They consist of transitory tetanic contractions of single groups of muscles, or of all the muscles of the body, on the application of a sensory stimulus. The less developed the abnormal condition of the spinal cord is, the more limited are the convulsions, and the stronger is the stimulus necessary to induce them. When, owing to an increased development in the abnormal condition, or to an increase in the strength of the stimulus (the stimulus being supposed to be applied to a limited portion of the skin), the reflex convulsions extend over a wider and wider area, they take the following course (Pflüger) :—They are first manifest in the muscles, the motor fibres of which arise in the cord on the same side and at the same level; then they spread to the muscles supplied by the fibres of the opposite side, but still only to those which are symmetrical with the muscles of the side first affected, and they are never more intense in the latter than in the former ; afterwards the convulsions affect muscles supplied by fibres given off at levels which are nearer and nearer to that of the medulla oblongata ; and, finally, the muscles supplied by all fibres enter into general tetanic convulsions, which, owing to the superior strength of the extensors, give rise to the appearance known as *stretching convulsions*. The fibres proceeding from the medulla oblongata may, without any such great extension of the reflex processes, be implicated in convulsions of a reflex nature, as will be shown below.

In poisoning by strychnia, the slightest disturbance of the patient, such as by a draught of air or a vibration of the couch, is enough to induce a paroxysm. It has recently been observed that, during the condition of apnœa, the reflex convulsions characteristic of strychnia and similar poisons do not occur (Rosenthal and Leube, Uspensky).

In order to understand reflex activity, it is necessary to suppose a union of motor and sensory ganglion-cells, and, moreover, a union in manifold ways. As direct anastomoses of these cells

do not occur (Deiters), this union can only be effected by means of the above-mentioned grey network of fibres. But since this network apparently unites all the ganglion-cells of the spinal cord together, while it is certainly possible to understand the extension of the reflex process to all the muscles of the body, as occurs in the general convulsions of strychnine poisoning, it is as difficult to see how the reflex process is ever limited and localised, or how it results in orderly acts, as it is to understand the isolated conduction of sensations to the brain, or the voluntary production of isolated movements in the trunk, to which reference was made on p. 477.

In order, therefore, to reconcile the physiological possibilities with the anatomical facts, it is necessary to assume that under ordinary circumstances there exists throughout the network of fibres a very great resistance to conduction, so that the excitation or impression, even at a short distance from the sensory cell, which had been directly stimulated, becomes reduced to an almost imperceptible strength. In consequence, excitation can only be distributed (*a*) in the neighbourhood of the stimulated cell, causing limited reflex actions, (*b*) along paths where conductivity is more perfect, and which do not originate in the fibrous network at too great a distance from the point of stimulation. Such paths of more perfect conductivity are, apparently, the fibres which were described as emerging from the network and running in the white substance to the brain. In this way the isolated conduction of sensibility, as well as that of voluntary impulses to movement, become intelligible. The latter sort of impressions might be supposed to descend along a fibre of the white substance and to pass into the grey network, where they would be able to enter those motor cells only which were in the immediate neighbourhood of the point of entrance.

The production of orderly, purpose-like reflex movements remains unexplained on this theory, since it is not certain that, in such movements, the impressions are transferred to the motor cells in the immediate vicinity. It must at least be first shown that the situation of the cells is such that the motor cells respond to the stimulation of the sensory cells nearest them by the most perfect movements for the purposes of defence, an arrangement which is, of course, quite possible. It is, however, quite as probable that, by an inherited perfection of organization,

conduction from every sensory cell in the network is especially favoured in certain directions (by a diminution of resistance in those directions), whereby purpose-like movements are subserved or that combinations are formed, more readily capable of conducting, by means of the fibres of the white substance.

The abnormal extension of the reflex process, first of all to neighbouring motor cells, then to motor cells more remote, and finally to the whole number of them, would further be explained by supposing a diminution of the above-mentioned resistance to conduction, which strychnia and the pathological causes of tetanus might be able to bring about in an extraordinary degree. If this were the true explanation, the power of referring sensations to definite localities, and of producing, voluntarily, local movements, would also be prejudiced; but concerning this we have no exact information.

This hypothesis admits, on the other hand, the possibility of the existence of influences capable of increasing the resistance to conduction, and therefore, of (1) rendering more difficult the production of reflex acts, and (2) rendering keener the powers of localising sensations and voluntary movements; and such influences have in fact been demonstrated.

After it had been noticed that the power of reflex action in the region belonging to the spinal cord became more regular and stronger after separation of the brain, certain organs were discovered to exist in the latter which constantly act prejudicially upon the reflex power of the cord, viz. Setschenow's '*inhibitory centres for reflex movements.*' If, by means of a metronome, the time be measured which elapses between the application of a continuous (chemical) stimulus and the commencement of the resulting reflex action, it will be found to be greater, with the same stimulation, according as the reflex powers of the central organ are slighter, since the stimulus does not acquire an intensity sufficient to liberate the reflex movement until after it has been applied for some time. It will be found that the time between stimulation and the movement induced by it is less, or, in other words, that the reflex power of the cord is greater, after separation of the brain at a point below the optic lobes; but that the reverse obtains on stimulation of the brain, and especially of the optic lobes, by means of salt solution, or blood, which, according to Setschenow, acts as

a stimulant to the central organs. The optic lobes, there-
fore, exert a constant inhibitory action upon the reflex powers
of the spinal cord, which, according to the above hypothesis,
must be due to an increase in the resistance to conduction
along the grey fibres of the network. Similar inhibitory
centres may be demonstrated to exist in mammals (Simonoff).

The operation of certain depressers of reflex power (morphia, digitaline,
etc.) depends upon the stimulation of these centres which they are able to
bring about (Setschenow, Weil). Increased venosity of the blood, pro-
duced by suffocation, or stagnation in the vessels of the brain, also acts as a
stimulus upon them (Rosenthal and Weil).

The exalted activity of the reflex powers, which is seen after
section of the spinal cord in all parts below the line of section,
and which is especially noticeable by comparison of the two
sides of the body after unilateral section of the cord, was
formerly described as 'hyperæsthesia and hyperkinesia.' It
cannot depend entirely upon the removal of the inhibitory
centres, since the act of section, during which a stimulation of
the nerves which usually convey the inhibitory impression is
unavoidable, does not first depress and then exalt the reflex
function of the cord, as might have been expected, but, on the
contrary, first exalts and afterwards depresses it. It must,
therefore, be assumed that section, and the subsequent presence
of blood at the surface of section, and other, partially unknown,
stimulants, first of all excite and finally exhaust the reflex
apparatus (Herzen, Setschenow and Paschutin). This action is
one upon the grey substance, while the paths of conduction,
which descend from the inhibitory organs, run in the white an-
terior columns.

Hence we are not fully entitled to ascribe to the apparatus
inhibitory of the power of reflex action, a constant (tonic)
operation. But it follows from what was previously said that
the brain has an inhibitory influence upon that power in some
other way. While a brainless animal performs with regularity
definite movements on the application of a certain stimulus, an
animal whose brain is uninjured has the power, evidently by
means of its will, of suppressing those movements as it pleases.
Just as an uninjured frog is not compelled to croak when its back
is stroked, so a man when awake can voluntarily suppress reflex
acts which he invariably performs when asleep, and to which,

even when he is awake, he feels 'an almost irresistible impulse.' Such acts are scratching the skin when the latter is irritated by itching; closing the eyelids when the conjunctiva is touched. (Exactly similar relationships exist in the domain of the brain.) There are, however, reflex actions upon which the will exerts no influence, as, for example, ejaculatio seminis on irritation of the penis, such acts being invariably those which cannot be induced by the will alone without the aid of the reflex power.

Another kind of inhibition of reflex movements occurs, according to recent observations (Goltz, Setschenow, Nothnagel, Lewisson), on powerful irritation of the sensory nerves even of animals whose brains have been previously destroyed. For example, the before-mentioned reflex croaking does not take place if the skin of the frog be powerfully stimulated at any point. There must exist, therefore, fibres inhibitory of reflex movements which run from the periphery to the spinal cord.

Orderly reflex acts do not follow on *strong* stimulation of the trunks of sensory nerves, owing, probably, to the simultaneous irritation of the inhibitory fibres contained in the nerves (Fick and Erlenmeyer).

There are, then, three kinds of influence inhibitory of reflex movement: firstly, that exerted by Setschenow's centres; secondly, that exerted by the mental organs; and, thirdly, that exerted by centripetal fibres. There is no reason to suppose, with Danilewsky, that the first and second kinds are identical, for, in the first place, the centres of Setschenow in the frog do not form part of the cerebrum, which is undoubtedly the seat of consciousness; and, in the second place, the two kinds of inhibitory influence are essentially different, the will either allowing or preventing the production of *orderly* reflex acts, while Setschenow's centres seem only capable of influencing the degree and extent of *irregular* reflex movements.

All kinds of reflex movement presuppose that the *blood* in the vessels of the spinal cord is, to a certain extent, venous; hence apnœa prevents the occurrence of reflex movements (Rosenthal).

It has recently been sought to classify reflex acts according to the method of their liberation (Setschenow, Danilewsky). Those induced by means of touching are called 'tactile reflex movements,' to distinguish them from 'pathetic reflex movements,' or such as follow the chemical or otherwise destructive and painful irritation of the skin. These two sorts of

inducing, or liberating, impressions have, moreover, been thought to travel along different centripetal paths, since the reflex movements induced by them differ in their nature. Such a distinction—which may possibly be supported on anatomical grounds—would, at the same time, explain the difference which exists in the power of the mind to refer to their exact locality impressions of a tactile and of a painful nature—the former being local-ised by the mind with far more exactness than the latter, which appear to radiate or extend over a considerable surface beyond the point of appli-cation of the irritant. (This difference may, however, be explained in the manner given on p. 486). It would appear, further, that it is only reflex movements of a 'pathetic' nature which are capable of inhibition by means of Setschenow's centres; while 'tactile' reflex movements, on the other hand, can only be inhibited by means of the will. These differences will be again spoken of.

The slight knowledge which we possess concerning the paths in the spinal cord along which the characteristic operations of that organ proceed, has been gained partly by direct experiment, partly from observations of pathological conditions, and partly from a study of anatomical arrangement. The experiments referred to consist mainly in observing the effects of partial section of the cord, such as unilateral section, section of in-dividual white or grey columns, section at different levels on the same or on opposite sides, etc. The method mentioned on p. 346 for the discovery of paths of conduction, viz. by stimulation, cannot be applied in the case of the spinal cord, if it be true, as some observers state, that the cord is not irritable to direct mechanical and electrical stimuli (Brown-Sequard, Schiff, Van Deen, S. Meyer). It must be remembered, however, that this statement is opposed by others (Fick and Engelken, Giannuzzi). For, assuming the statement to be true, no stimuli applied to the spinal cord, except those of a chemical nature, which appear to be partially *active*, will produce any results if they do not directly excite the root-fibres of some spinal nerve which happens to be traversing the cord at the point of stimu-lation.

The fibres of the cord proceeding from the vaso-motor centre must be excepted in the above statement, as every stimulation of spinal cord produces narrowing of all the arteries supplied by fibres given off below the point of stimulation (Ludwig and Thiry). Moreover, all stimulations of the substance of the cord, as was mentioned on p. 76, cause reflex irritation of the vaso-motor centre, and raise the blood-pressure (Ludwig and Dittmar). Should the apparent inability of electrical and mechanical stimuli to irritate the cord be really established, notwithstanding the

assertions to the contrary of Fick and Giannuzzi, it ought rather to be ascribed to an overpowering irritation of such inhibitory fibres as happen to come in the way of the stimulus than to an absolute inability on the part of any conducting portion of the cord to respond to stimulation. In the latter case, it must be supposed that only axis cylinders of the first kind have the general properties of extra-central nerve-fibres, and that the remaining, specially central, fibres cannot be irritated by the most important nervous stimuli. In order to express that the conducting substance of the cord is only capable of conduction and not of irritation, the terms 'æsthesodic' (capable of conducting sensory impressions) and 'kinesodic' (capable of conducting motor impressions) have been applied to it.

From the effects of partial division of the cord in various ways (Brown-Sequard, Schiff, Setschenow, and others) the following conclusions have been drawn. 1. The conduction of localised sensory impressions, and of motor impressions which are voluntarily restricted to definite sets of muscles, is effected through the white substance. Partial section of the latter severs the connection between the mind and individual regions of the skin and individual groups of muscles. Hence result insensibility to tactile impressions—anæsthesia, and paralysis of voluntary motion. The paths which subserve conduction remain on the same side of the cord as far as the brain, *i.e.* they do not cross the middle line of the cord. The conduction of sensory impressions takes place through the posterior white columns, that of motor impressions through the anterior and lateral white columns. 2. The 'pressor' fibres, which proceed from the posterior extremities, course along the lateral columns, and cross the cord partially (Ludwig and Miescher). 3. The conduction of painful impressions, and of involuntary (and especially reflex) motor impulses, takes place through the grey substance, in its whole extent, without any distinctions of sensory and motor tracts. Section of the grey substance, therefore, produces, among other things, a condition in which painful operations cause sensations of touch, but not of pain—'analgesia.' Such a condition frequently supervenes during the narcosis of chloroform, in which case the knife of the surgeon is felt, but no sensation of pain is experienced. This result of section of the grey substance is not restricted to sharply defined regions of the body, as are the results of section of the white substance, but is somewhat regular in all the parts supplied by nerves which enter the cord below the point of section; and it is the

more complete according as section has included more of the grey substance.

These experiments agree well with the phenomena of reflex action and with the discoveries of anatomists. According to all that has been said, a normal, sensory stimulation, a 'tactile stimulus,' after leaving the sensory ganglion-cell, would not travel for any distance in the grey network of fibres, but would speedily make its way into a fibre of the white posterior columns, along which it would be conducted to the organs of the mind, and would there give rise to a localised sensation. The conduction of an impulse along the fibres of the grey network, in addition, stimulates a number of motor cells and, mediately through them, their attached fibres, by which means an orderly reflex act is produced. This reflex act may be inhibited, in some unknown way, by a descending excitation from the will travelling down the white anterior columns from the brain. In like manner, the will, by means of an impulse transmitted down the white anterior and lateral columns, may induce in the grey fibrous network an excitation of limited extent, by which certain motor cells and fibres can be rendered active, and a voluntary and restricted movement produced.

Violent ('pathetic') stimulations, on the contrary, produce a stronger excitation of sensory·ganglion-cells, an excitation which is capable of more extended conduction through the grey substance than that induced by a more moderate stimulation, and which may even affect the whole of the fibrous network. In the first place a far greater number of the fibres of the posterior columns derived from the network will, consequently, be stimulated, though not all to the same degree, since those fibres which are nearest the excited cell will be more powerfully stimulated than those more remote, on account of the resistance offered by the grey network. Hence results a less exact localisation in consciousness of the sensation (diffused sensations). In the second place an extended conduction of the state of excitation through the fibrous network must call into activity a greater number of motor apparatuses, and, in consequence, produce extended, irregular, reflex movements, an effect which may be prevented by an inhibitory impression proceeding from Setschenow's centres and descending in the white substance. Finally, the transmission of the state of excitation through the

grey substance to the brain seems (though it is still doubtful) to cause a sensation of pain.

In order to explain the phenomenon of orderly reflex movement it is necessary to assume the existence of certain combinations of ganglion-cells, in which an especially slight resistance is opposed to conduction. In this way arise certain *co-ordinations* of motor elements, which can apparently be called into activity, not only in a reflex manner, but also by the will, so that the will, in intentional, purposive movements, need not have stimulated each individual fibre supplying the muscles, but may have simply rendered active the same apparatus as would have been brought into play in the reflex production of the same movement. If this were not so the mind would have more work than it could accomplish in the production of the innumerable muscular movements required in such an apparently simple operation as walking.

It is not yet satisfactorily settled whether the spinal cord possesses *automatic* apparatuses in addition to those already mentioned. The following automatic functions, which have been ascribed to the spinal cord, will now be discussed.

1. *The Maintenance of the Tonus of Voluntary Muscles.*

By '*muscular tonus*' is understood a constant, slight, and involuntary contraction of all the muscles of the body, but especially of those of animal life, which is dependent upon the nervous system. All the appearances which are usually received as proof of the existence of this constant tonus are, however, capable of explanation in other ways. Thus, the retraction of severed muscles, which was supposed to be due to it, takes place when the nerves supplying the muscles have been previously divided, and is merely due to the fact that muscles in the body are extended somewhat beyond their natural length (p. 242). Again, distortion of the face after paralysis of the facial nerve on one side need not depend upon a deficiency of muscular tonus on that side, but upon the fact that, after contraction of the muscles of the opposite side has once occurred, there are no means of re-extending the muscles to their original shape (p. 257). But the assumption of any such real automatic tonus may be directly disproved by first

of all making a preparation in which an extended muscle is still connected with its motor nerve and the central nervous system, and then dividing the nerve, when it will be noticed that the muscle does not become in the slighest degree elongated (Auerbach, Heidenhain).

On the other hand, individual voluntary muscles may, under certain conditions, be shown to be under an involuntary and weak contraction, which is not, however, automatic, but reflex in its nature. If a frog be vertically suspended, after having its brain separated from its spinal cord, and the nerves of one of its hinder legs be divided, it will be noticed that the injured leg hangs more loosely than the uninjured one. The same results follow if, instead of dividing the whole sciatic plexus of nerves, the posterior roots alone be cut. Hence it must be concluded that the slight flexion of the uninjured limb is not due to an automatic, but to a reflex action which is liberated by means of the sensory fibres of the limb (Brondgeest), and the necessary irritation of which appears to proceed from the skin (Cohnstein). This contraction does not affect all the muscles of the limb, nor has it been shown to exist at all in the ordinary posture of the body. In the first place, as may be proved, it only affects the flexors; and in the second it is but another form of the better known phenomenon that a brainless frog strives, in all positions of body, to retract its legs. It has not yet been proved that, after the legs have been drawn up as in sitting, contraction of the flexors continues in the same manner as during suspension, when retraction, on account of the weight, cannot be maintained, except to a slight extent, for any length of time (Hermann). Hence Brondgeest's phenomenon is to be regarded merely as the special continuance, under abnormal circumstances, of a contraction of reflex origin, which is usually transitory. We must conclude, therefore, that the existence of a 'muscular tonus' is not yet established.

The influence of section of the posterior roots in diminishing the irritability of the anterior (p. 353), which has recently been contested by Grünhagen and G. Heidenhain, may be explained by reference to the above-mentioned phenomenon (Steinmann and Cyon).

2. *The Maintenance of the Tonus of Smooth Muscles.*

A. The tonic contraction of the dilatator-fibres of the pupil (p. 377) and the smooth optic muscles of Müller, which ceases on section of the sympathetic cord in the neck, is said to be under the influence of the spinal cord. The automatic centre for this influence is said to lie in the neighbourhood of the lower cervical and upper thoracic vertebræ ('centrum ciliospinale,' Budge ; 'centrum occulo-spinale,' Bernard); because, in the first place, as may be shown, the sympathetic cord derives the fibres concerned from the anterior root of the spinal nerve of that locality ; and, in the second place, a condition of paralysis or of irritation of the cord in that vicinity is accompanied by corresponding phenomena in the eye ; paralysis, for example, being marked by contraction of the pupil, etc. These circumstances, however, as is easily seen, merely prove that the region of the cord referred to is concerned in the *conduction* of the necessary impressions, and not that it is their place of origin. Moreover, since section of the cervical portion of the cord causes contraction of the pupils (Schiff), and prevents dyspnœic dilatation of them (Salkowski), it is evident that some portion of the fibres concerned in the production of this result, and the cause of their tonic excitation, must be above the spinal cord, somewhere in the medulla oblongata. The ciliospinal centre, therefore, is analogous in function to the rest of the grey substance of the cord, and must be regarded merely as the *proximate* origin of the fibres to the eye, and, possibly, as reflex in function.

B. The *tonus* of arteries (p. 75) is also known to be dependent upon the integrity of fibres which are derived from the spinal cord, for unilateral section of the cord causes dilatation of all the arteries of the same side below the level of section. A centre for all these fibres is situated in the medulla oblongata, as will be explained below; but in this case also the grey substance appears to contain proximate centra of a reflex nature, to which the descending vaso-motor fibres first proceed. The cord must even be supposed to have a share in the tonic excitation of the fibres, for the arterial dilatation following division of the cord below the level of section is not permanent, but soon gives place

again to contraction; and permanency of dilatation is not secured until the cord below the point of section is destroyed, when the animals experimented on die, if the area over which dilatation has taken place be sufficiently large (Le Gallois, Goltz). Moreover, poisoning by means of strychnia causes contraction of the arteries which have been previously dilated by dividing the cord above (Schlesinger). The vaso-motor nerves descending from the medulla oblongata, as well as the 'pressor' fibres proceeding to it, are contained in the lateral columns of the cord (Dittmar).

C. The *tonus* of *sphincters.* The sphincter ani is constantly contracted, for, in order to overcome its resistance, it is necessary to distend the rectum with fluids to a greater extent when the nerves supplying it are intact than when they are divided (Giannuzzi and Nawrocki). The central nervous organ concerned in this constant contraction ('centrum ano-spinale') is situated in the spinal cord, in the dog opposite the lower third of the fifth lumbar vertebra (Budge, Giannuzzi, Masius), in rabbits between the sixth and seventh lumbar vertebræ (Masius). The sphincter of the bladder and its tonus have already been discussed on p. 118, where it was stated that neither the tonus nor even the sphincter-muscle itself have been distinctly proved to exist. The chief cause of the closure of the bladder, viz. the contraction of the urethral muscles (Budge), is most probably reflex in its nature. The central organ concerned in this closure ('centrum vesico-spinale') is situated immediately below the ano-spinal centre (Masius). The tonic closure of rectum and bladder is regulated by fibres proceeding from the brain (Masius), just as are the other regular reflex acts over which the spinal cord presides.

Not a single automatic centre, therfore, can with certainty, or even with probability, be assumed to exist in the spinal cord; all the phenomena supposed to depend upon such centres are capable of explanation as processes of the nature of 'orderly reflex actions.'

The schema of the construction of the spinal cord, represented in the diagram, may serve to make clearer what has been said concerning the physiology of this portion of the nervous. system. The figure represents an antero-posterior vertical section, taken a little to one side of the middle line.

2. Encephalon.

The continuation upwards of the spinal cord, consisting of medulla oblongata, cerebellum, the so-called cerebral ganglia (corpora quadrigemina, thalami optici, corpora striata, etc.), and

Fig. 49.
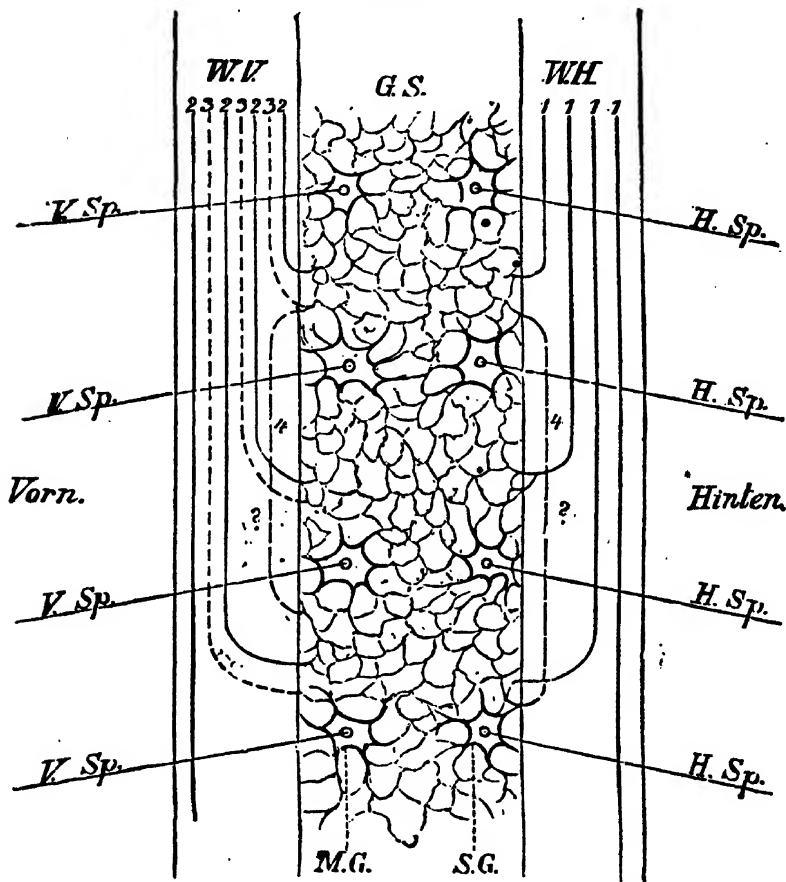
G s grey substance, W V white anterior column, W H white posterior column, V sp. anterior root-fibres, and H sp. posterior root-fibres, of spinal nerves. M G motor ganglion-cell of grey anterior cornu, S G sensory ganglion-cell (?) of grey posterior cornu, 1 1 1 1 sensory fibres, 2 2 motor fibres, 3 inhibitory fibres, 4 4 co-ordinating fibres (?).

the cerebral hemispheres, contains a great number of central organs concerning the functions and combinations of which extremely little has been discovered. The cerebral hemispheres contain the organs concerned in the psychical functions, as will be shown hereafter.

One of the chief objects of the physiology of the central nervous system is to investigate the connections between the organ of the mind and the peripheral end-organs, viz. sense-organs and muscles. As far as spinal nerves are concerned it has already been shown that they do not proceed directly to the surface of the cerebral hemispheres; but that they first enter the grey substance of the cord. This substance is then connected with the brain—but still, as will be presently explained, not with the surface of the cerebrum—by means of the longitudinal fibres of the white columns.

Cranial nerves, also, do not communicate directly with the surface of the cerebrum, but first enter certain intermediate central organs, a general view of which is contained in the following statements.

The grey mass covering the cerebral hemispheres gives off the following systems of fibres, which form the white substance of the hemispheres:—1. Fibres uniting together various regions of the surface on one side (so-called 'associating fibres'). 2. Fibres uniting symmetrical, and perhaps also unsymmetrical, regions of surface of the two hemispheres (so-called 'commissural fibres' passing through the corpus callosum and the anterior commissure). 3. Radiating fibres running towards the above-mentioned cerebral ganglia or grey masses lying in the interior of the brain ('peduncular fibres'). The third system must constitute the bond between the organ of mind and the external world, that is to say, if there is not yet another system (which Broadbent maintains) consisting of fibres which run uninterruptedly from the posterior part of the grey matter through the crura cerebri into the white substance of the cord.

The ganglia at the base of the brain are directly connected with nerves (anterior cranial nerves) and with one another. Finally, the strongest bonds of union pass, by means of the peduncles of the brain, to the cerebellum, and to the grey substance of the medulla oblongata and the spinal cord, and, therefore, to the proximate termination of almost all peripheral nerves.

If we regard as the object of all nervous combinations the projection of the surface of the body, in its motor and sensory aspects, upon the plane of the mental organs, the following schema of this projection may be drawn (Meynert):—The first system of projection, perhaps better described as the

inner, unites the cerebral cortex with the large ganglia at the base of the brain (the radial system of fibres); the second system of projection, or the middle system (the peduncles, etc.), unites the basal ganglia with the grey substance of the spinal cord and the analogous portion of the medulla oblongata (viz. the 'central grey tube,' so called because the substance composing it lies about the central canal of the cord and its continuation—the *calamus scriptorius*, floor of the fourth ventricle, aqueduct of Sylvius, and third ventricle); the third system of projection, or the external, is constituted by the peripheral nerves. The second is weaker than the others; hence at the points of union of the three systems there is noticed between the internal and middle a reduction, and between the middle and external again an increase, in the number of fibres. In the middle system a crossing, probably of all the fibres, takes place, *i.e.* the fibres cross the middle plane to reach the opposite side of the body.

This schema, as might be expected, does not hold in its entirety; deviations from it are observable especially in the case of the anterior cranial nerves, in which there appears to be no organ corresponding to the central grey tube, and, therefore, no middle system of projection.[1] Moreover, the fibres above mentioned, which pass from the grey matter of the cortex direct to the central grey matter, would offer an example of deficiency of the middle system of projection.

The cerebellum forms a centre, laterally situated, which communicates with all the rest, and from which, also, arise nerve-fibres of the external system (portions of the trigeminus and acoustic nerve).

Fig. 41.
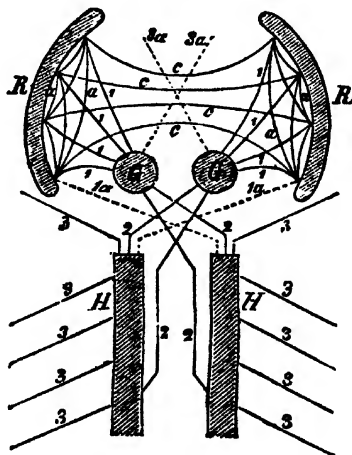
The annexed diagram serves to explain the three systems of projection: **R** is the grey substance of the cerebral cortex, **G** the ganglia at the base of the brain, **H** is the central grey tube, 1, 2, 3 are the fibres of three systems

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[1] Many observers believe that, in the nerves of special sense, the peripheral ganglion-cells are the organs which correspond to the central grey tube, considering, for example, the optic fibres as the *middle* system of projection and the radial fibres of the retina as the external series.

of projection, *a* are associating, and *c* are commissural fibres. The dotted fibres represent the above-mentioned deviations; for example, 3*a* represents the optic fibres, and 1*a* the combining fibres of Broadbent.

The combinations of the ganglia at the base of the brain one with another and with the grey substance of the spinal cord, and with its cerebral analogue, are the most difficult to determine, and form the weakest portion of the anatomy of the encephalon. Where the spinal cord becomes medulla oblongata the central canal of the former makes its way to the surface posteriorly in the calamus scriptorius, and forms a shallow groove in the floor of the fourth ventricle. The grey substance surrounding the canal, at the same time, reaches the posterior surface and lies spread out on the floor of the groove, the anterior cornua being external to the posterior. More superiorly the grey substance assumes the form of scattered grey masses, the so-called 'nuclei' of the posterior cranial nerves, which are clearly the analogues of the grey substance of the spinal cord. The main body of the medulla oblongata consists of white columns, the continuations of the white columns of the cord, which run in part to the ganglia at the base of the brain, viz. to the corpora quadrigemina and through the crura cerebri to the thalami optici, corpora striata, and lenticular nucleus, and in part to the cerebellum. From the white posterior columns of the spinal cord those fibres contained in the funiculi graciles and processus cuneati pass through the crura cerebelli to the cerebellum; the rest pass through the external bundles of the pyramids and the crura cerebri into the cerebrum (some, as was mentioned above, passing directly to the cortex of the posterior portion); and a small number of fibres run directly into the trigeminal nerve, which thus gets a spinal root. The anterior and lateral columns run partly through the pyramids and crura cerebri to the corpora striata and lenticular nucleus (and, possibly, in part direct to the cortex of the cerebrum), partly to the corpora quadrigemina and through the tegmentum to the optic thalami, and partly through the corpora restiformia and the crura cerebelli to the cerebellum. The cerebellar hemispheres, which, according to what has just been said, communicate with all the white columns of the cord through their peduncles, are in addition united with the pons, and hence with each other, by means of the crura cerebelli ad pontem; and

also to the cortex of the cerebrum, by the crùra cerebelli ad corpora quadrigemina, which do not really communicate with the grey substance of the corpora. The medulla oblongata contains, in addition, the hemispherical olivary bodies, about the relations of which little is certainly known.

The following statements embody what has been discovered concerning the origins of the cranial nerves:—

First pair (*Olfactory*). The olfactory tracts lying at the base of the anterior lobe of the brain, and becoming continuous with the olfactory bulbs, are the rudiments of the olfactory lobes of the lower animals—largely developed lobes of the brain analogous in structure to the cerebral hemispheres. Their white fibres communicate with various portions of the cortex of the cerebrum, and, according to some, with the corpora striata also. From the bulbs arise the olfactory nerves proper, which perforate the cribriform plate.

Second pair (*Optic*). The optic tracts arise in part from the corpora geniculata externa and from the thalami optici, and in part from the corpora geniculata interna, and from the anterior corpora quadrigemina. Bending round the crura cerebri, they then form the optic chiasma, in which, according to some, one half, and according to others, all, the fibres of each tract cross over to the opposite side (p. 417).

Third pair (*Motores oculi*) and

Fourth pair (*Trochlear* or *pathetic*) arise on each side in the neighbourhood of the aqueduct of Sylvius, from a grey nucleus, common to both, which communicates with the above-mentioned corpora quadrigemina, and also through the crus with the lenticular nucleus. While the *third nerve*, piercing the crus to its under surface, emerges close to the pons, the *fourth* passes upwards, perforates the roof of the aqueduct, crossing at the same time to the opposite side, and bends round the crus, after the fashion of the optic tract, to appear on the surface below.

Fifth pair (*Trigeminal*). The fibres of this nerve have very various origins. *a.* On a level with the point of exit from the pons is the so-called 'trigeminal sensory nucleus,' the ganglionic cells of which are small, which is analogous to the posterior cornu of the grey substance of the cord; from it certain of the fibres originate. *b.* The ascending root is derived from the posterior column of the cord—and from a portion at least as low down as the middle of the neck,—the fibres springing from the grey substance of the posterior cornu and running in the white posterior columns. At the side of the medulla the fibres run for some distance very superficially. This very sensitive part, situated close behind the processus cuneatus, and sometimes but slightly developed, is the tuberculum Rolandi. *c.* Descending roots, viz. (1) from the large-celled 'trigeminal motor nucleus,' in the neighbourhood of the corpora quadrigemina, concerning the further connections of which with the ganglia of the brain nothing is known; (2) from a collection of large vesicular cells (similar to the cells of the spinal ganglia) at the side of the aqueduct of Sylvius; (3) from the locus cæruleus which

lies beneath the *substantia ferruginea* in the upper part of the floor of the fourth ventricle, the fibres being crossed. *d.* Fibres from the cerebellum, running in the crura cerebelli ad corpora quadrigemina.

Sixth pair (*Abducens*). The fibres of this nerve arise from a large-celled nucleus at the bottom of the groove in the floor of the fourth ventricle, at its anterior part. The further connections of this nucleus, which supplies fibres to the facial, are unknown.

Seventh pair (*Facial*). This nerve is derived from a nucleus similar to the one last mentioned, though situated somewhat lower, but receives a number of fibres also from the nucleus of the *sixth* nerve. Another, descending, set of fibres comes from the lenticular nucleus of the opposite side of the body. The connections of the nucleus of this nerve are unknown.

Eighth pair (*Auditory*). This nerve receives fibres chiefly from three interdependent nuclei, which lie on a level with the broadest (middle) portion of the floor of the fourth ventricle, between and in front of the corpora restiformia. Fibres both from these nuclei and from the trunk of the auditory nerve may be traced into the crura cerebelli and into the cerebellum, but the other relations of the fibres of the auditory nerve are not as yet known. A portion of the fibres cross between their nucleus of origin and their place of exit.

Ninth pair (*Glosso-pharyngeal*) and

Tenth pair (*Par vagum, pneumogastric* or *vagus*) arises from nuclei, which are, in part, common to both, situated in the lower half of the floor of the fourth ventricle, and in the substance of the medulla oblongata near the olivary bodies. These nuclei supply fibres to the spinal accessory also. Their connections are not known.

Eleventh pair (*Spinal accessory*). In addition to the fibres from the nuclei just mentioned, this nerve is supplied from an elongated nucleus lying along the external surface of the anterior cornu and reaching as far down as the fifth cervical vertebra. The fibres leave this nucleus in a great number of roots, which lie in a special line down the lateral column of the spinal cord between the anterior and posterior roots of the cervical spinal nerves. This line is somewhat spiral, being more posterior below.

Twelfth pair (*Hypoglossal*). The fibres of this nerve arise, for the most part, from two large-celled nuclei, situated deeply in the substance of the medulla oblongata, on a level with the lowest portion of the floor of the fourth ventricle. Some of the fibres appear to arise higher up in the brain without touching the nuclei. Certain observers have maintained the existence also of connections with the olivary bodies.

The statements of anatomists are too incomplete and insecure for the establishment of any theory concerning the functions of the various parts of the brain. Theories have, however, been set up notwithstanding the deficiency of facts at our disposal. Such a one, for example, is that of Meynert, according to which that division of the crura cerebri which is known as the *basis* or pedunculus (in the limited sense) which

is connected with the lenticular nucleus and corpora striata, and which is developed in the various members of the animal series proportionately to the cerebral hemispheres, is concerned in the conscious reception of sensations and in the production of movements; while that portion of the *crus* which is known as the *tegmentum* (Haube), and which communicates with the optic thalami and the corpora quadrigemina is concerned in the reflection of impressions from the optic nerves into the motor apparatus.

Physiological experiments conducted in these regions are most indefinite. The usual plan of investigation, viz. that of applying stimuli to the brain-substance, leads either to negative results (p. 484), or, if electrical stimulation is used, to results which, owing to the unavoidable dispersal of the currents in numerous directions, are not sufficiently localised to form the basis for trustworthy conclusions. In the place of exact observations after section and stimulation of different regions, we have here the far less refined method of observation after lesions,—lesions induced in the most delicate and complicated organ of the body by means so absurdly rough that, as Ludwig has forcibly put it, they may be compared to injuries to a watch by means of a pistol shot. The results obtained in this way are attributable to the most diverse causes; for, apart from the fact that it is impossible to localise the lesion itself, the results may be due to irritation of centres, paralysis of centres, stimulation of conducting apparatus, or paralysis of conducting apparatus, without our being able to say to which. Hence the interpretation of even those phenomena which are constant in their occurrence is always uncertain.

The third and best method of investigation which is possible is the observation of cases of disease in which the exact nature of the lesions is accurately ascertained after death.

The facts which may be considered in some degree established are the following :—

A. Medulla Oblongata.

In the medulla oblongata essentially the same arrangement of parts is noticed as in the spinal cord. The grey substance, the connections of which with that of the spinal cord, and with

the cranial nerves from the sixth (abducens) downwards, have already been described, is, without doubt, the seat of manifold reflex processes in which those nerves are implicated, and of a number of motor impulses, some of which (if not all, as some think) are to be regarded as reflex in their nature, others as automatic. The functions in which the medulla is concerned are of such importance to the whole organism that injuries of this portion of the encephalon are more dangerous to life than those of any other region of brain or spinal cord.

1. *The Centre for the Involuntary Movements of Respiration, and for the Convulsions of Dyspnœa.*—Lesion of a limited region of the floor of the fourth ventricle at the apex of the calamus scriptorius causes sudden cessation of respiration, and instant death to warm-blooded animals. This region is called *le nœud vital*, or *point vital* (Flourens). It extends on both sides of the middle line ; and, if the lesion affect one side only, the respiratory symptoms affect the corresponding side of the body alone.

According to more recent statements (Gierke) the structure, injury to which abolishes respiration, does not consist of a mass of ganglia, but of two bundles of fine nerve-fibres, which spring in part from the vagus-fibres entering them, and in part from the nuclei of the vagus and trigeminus, and which run towards the spinal cord, whence the proper respiratory nerves arise. While extirpation of the individual nuclei is not alone sufficient to cause respiration to cease, destruction of this, partly intercentral and partly, even, merely centripetal, combination between vagus, trigeminus, and spinal origin of respiratory motor nerves, produces paralysis of respiration. The view that this nervous union constitutes essentially the ' respiratory centre ' seems, however, inadmissible, for the *rhythmical* character of the excitation can scarcely originate otherwise than in some ganglionic apparatus. It is quite possible that this ganglionic apparatus is situated in the spinal cord itself, if, as is stated, animals poisoned by strychnia still breathe after section of the cord in the cervical region. (P. Rokitansky.)

It is not yet established whether this centre liberates the rhythmical movements of respiration automatically, or whether its activity is dependent upon the excitation of centripetal nerves, and is, therefore, reflex in its nature (p. 169). The respiratory centre is the only centre concerning which the conditions of the automatism (or of the reflex powers) are at all fully understood. Its activity requires :—1. The presence of oxygenated blood, without which irritability disappears. 2. A certain relationship among the gases of the blood, which rela-

tionship acts as a stimulus ; the smaller the amount of oxygen, and the larger the amount of carbonic acid, present in the blood, the more intense becomes the activity of the centre, and the greater the number of muscles which are brought into play (Dyspnœa) ; if the amount of carbonic acid present sinks below a certain point, the activity ceases altogether (Apnœa). More exactly speaking, the respiratory centre consists of two centres, the rhythmical activities of which, although apparently independent as to strength, alternate as to the time of their phases, viz. one being connected with the inspiratory and the other with the expiratory muscles. Each supplies a definite group of muscles, the members of which, however, are not all equally implicated in movement, more or fewer being rendered active according to the strength of the exciting cause, which varies in proportion as reflex processes are extended in the spinal cord (pp. 479, 486). Moreover, these centres possess accelerating and inhibitory nerves, in the sense in which the terms were explained on p. 483. Stimulation of those nerves, whose course has already been given (p. 167), does not seem in general to increase or diminish the activity of the centre, but merely to modify the distribution of the activity in time. The fibres which produce on irritation slowing of the movements of inspiration cause at the same time quickening of those of expiration, and *vice versâ*. With the aid of the conception developed at page 480 we may form the following conjecture as to the influence exerted by these respiratory nerves (Rosenthal) :—Both in the case of inspiration and expiration a resistance to the discharge of the energy tending to excite movement must be supposed, which brings about the rhythm of the action. If, now, it be assumed that an increase of resistance in the one case increases the force of stimulation in the other ; and that, further, stimulation of the vagus-fibres weakens the inspiratory resistance, while that of the superior laryngeal fibres strengthens it, all the phenomena mentioned in Chapter IV. may be accounted for. The normal inspiratory resistance must be supposed to be so slight that no stimulation to expiration, and, hence, no *active* expiratory movements, occur. If the inspiratory resistance be increased, by stimulation of the slowing, or section of the quickening fibres, in the first place, inspiration becomes seldomer and deeper, and in the second,

owing to the activity of expiratory stimulation, expiratory resistance is overcome, and *active* expiratory movements follow— a result which is more marked, both in the number and strength of the expirations, the stronger the stimulus. If, on the contrary, the inspiratory resistance is diminished, by stimulation of the vagus, in the first place inspiration becomes quicker and shallower, and finally tetanic, and, in the second, if expiration have previously been effected by active (muscular) movements, such active movements entirely disappear. Finally, if stimulation be increased, *i.e.* if the blood become poorer in oxygen or richer in carbonic acid, it is clear that both inspiration and expiration must increase in frequency, strength, and in the number of muscular movements involved; or, in other words, the condition of *dyspnœa* supervenes, in which *active* expiratory movements occur, such as did not previously take place (p. 169).

The above conditions may be best illustrated by the example already given of gas conducted through a tube under water, only, in this case, the gas must be supposed to be led through a *forked* tube, the limbs of which dip into different fluids. One of these fluids—that representing the normal resistance to inspiration—must be supposed to be considerably less cohesive than the other, representing that of expiration. Irritation of the vagus corresponds to diminution, and irritation of the laryngeus to increase, in the cohesiveness of the first fluid. Dyspnœa corresponds to increase of the pressure under which the gas is forced through the tube. The bubbles which stream up through the first fluid represent the nervous impulses transmitted to the inspiratory apparatus; those which ascend in the latter to the impulses transmitted to the expiratory mechanism. The illustration shows at the same time that, for simple reasons, in the case when bubbles rise in both tubes (*i.e.* when inspiration and expiration are both *active*), they ascend alternately, first in the one and then in the other.

The increase in the frequency of respiration under increased temperature (p. 167) may be produced by raising the temperature of the brain alone, which is accomplished by placing the carotids in heated tubes (Fick and Goldstein). It is therefore considered to be dependent upon changes occurring in the respiratory centre. At high temperatures artificial respiration does not produce apnœa (Ackermann).

If excitation of the respiratory centre reaches an abnormal strength, other muscles besides the normal and accessory muscles of respiration are brought into play, viz., in the first place, the muscles of the jaws, as in gasping, and finally almost all the

muscles of the body, as in the general epileptiform convulsions attendant upon suffocation. This is clearly a mere case of extension of the condition of excitation throughout the grey substance of the medulla, and perhaps also of the cord; and, as a fact, other nervous centres in the medulla are implicated, as the centre for the dilatation of the pupils, the vaso-motor centre, and the cardiac-inhibitory centre. Some observers explain the phenomenon by assuming the existence of a special ' convulsion-centre' in the medulla.

According to recent researches, in which the medulla was directly stimulated, the above-mentioned convulsions occur on irritation of a region which (in rabbits) is bounded above by the corpora quadrigemina, below by the alæ cinereæ, externally by the locus cœruleus, and acoustic tubercle, and internally by the eminentiæ teretes. This region, which is stimulated to activity by the presence of asphyxial blood, is not supposed to be the real ' convulsion-centre,' but merely a point from which radiate impulses to movement, which are derived from a reflex convulsion-centre situated in the pons (Nothnagel).

These convulsions occur not only when the interchange of the gases of the blood is prevented, but also when the blood, or the substance of the brain, is deprived of oxygen or is saturated with carbonic acid, as, for example, when the blood in the blood-vessels of the brain stagnates in consequence of ligature of all the afferent arteries, or when excessive bleeding has occurred. These observations (Kussmaul and Tenner) have led to the designation of 'convulsions of anæmia,' a term which is now no longer admissible when the true nature of the process is understood (Rosenthal), and when it has been found possible to produce the same convulsions by causing venous blood to stagnate in the vessels (Hermann and Escher).

2. *The Centre for the Regulation of the Heart's Action.*— The centre whence the inhibitory vagus-fibres for the heart receive their stimulation (which, as was explained on p. 72, is possibly rhythmical in its nature) lies somewhere in the medulla oblongata, but its precise situation is not yet known. In warm-blooded animals the centre is constantly active, not, however, as has hitherto been assumed, automatically, but as a consequence of reflex stimulations; for section of certain centripetal nerves releases the 'tonus' of the vagus (p. 78), and, according to Goltz and Bernstein, irritation of them increases its inhibiting powers. It has not yet been determined

whether the accelerating nerves of the heart also, which will be described when the sympathetic system is treated of, have their centre in the medulla oblongata.

It is evident that some connection exists between the cardiac inhibitory and the respiratory centres; for during every respiratory act there occurs a stimulation of inhibitory vagus-fibres (Donders), which probably coincides with the close of inspiration, but the effects of which, on account of the 'period of latent stimulation' (p. 257), do not become manifest until the commencement of expiration (Pflüger, Donders.)

3. *The Vaso-motor Centre.*—The general vaso-motor centre lies certainly higher than the commencement of the cord, for section of the cord in the cervical region paralyses all the arteries of the body (Ludwig and Thiry). It extends in rabbits from about 3^{mm} above the calamus scriptorius to the upper portion of the floor of the fourth ventricle, but its upper boundary cannot exactly be determined; and is situated bilaterally, at some distance from the middle line, in that portion of the medulla which contains the continuation of the lateral spinal columns, in which, as has been already stated, the vaso-motor and pressor fibres run. It contains some large multipolar ganglion-cells (Owsjannikow, Dittmar). It is constantly in action, and its activity is either automatic or, perhaps, merely reflex. The facts in connection with this activity and the influence exerted upon it by the gases of the blood and by the regulating nerves have been already stated (p. 79). The fibres proceeding from the centre pass into the cord, and, after having probably been first interrupted by the grey substance in the manner indicated in the section on arterial tonus, leave it again, set by set, in order to be distributed to the arteries, for the most part along with fibres from the sympathetic system. Hence, section of the spinal cord causes dilatation of all the arteries in the regions below the point of section, while its irritation produces the opposite condition of contraction (Ludwig and Thiry), the former diminishing and the latter increasing the blood-pressure and temperature of the organism, and acting on the heart in a corresponding manner (p. 234).

Irritation of the crura cerebri causes contraction of all arteries (Budge). This circumstance does not disprove the former statement that the proper vaso-motor centre lies in the medulla; it merely shows that the cerebrum can exert some influence upon that centre—blushing and growing pale, due

to psychical causes (Budge); the reader should refer also to the effects of removal of the cerebrum upon the action of sensory nerves (p. 79).

4. *The Centre for the Dilatation of the Pupils, and for the Movements of the other Smooth Muscles of the Eye.*—The exact position of ·the centre which gives off fibres to the oculo-spinal region of the spinal cord is not known. The centre itself, wherever it be, is constantly active, and, possibly, owing to reflex stimulation. It is under similar influences to the respiratory and vaso-motor centres, dyspnœa, for example, being accompanied by dilatation of the pupils whilst the optic vessels become pale.

Many circumstances already alluded to seem to indicate a close connection between the four centres just discussed, especially their stimulation by a certain condition of the blood as to gaseous contents, the coincidence in the rhythm of their action, where such rhythm occurs, &c. (compare pp. 79, 169, and 379.)

5. *The Centre for the Movements of Swallowing.*—The proof that this centre is situated in the medulla oblongata chiefly rests upon the occurrence of convulsive movements of swallowing when that portion of the nervous system is under stimulation, and upon the anatomical fact that the nerves concerned in the act are derived from the medulla. The exact situation of the centre is not yet determined. The centre is only called into activity by reflex stimulations, and must therefore be put into the same category with the numerous apparatuses in the spinal cord for orderly reflex actions (p. 146).

6. *The Centre for the Movements of Mastication.*—The proofs of the existence of this centre in the medulla are similar to those in the last-mentioned centre, viz. the occurrence of trismus or cramps of the masticatory muscles under similar circumstances to those mentioned above. The centre resembles the spinal apparatuses for orderly reflex actions which are capable of use in regular voluntary movements.

7. *The Diabetic Centre.*—Lesions of a portion of the floor of the fourth ventricle near the middle line, and extending from a little above the calamus scriptorius to the broadest part of the groove, cause transitory diabetes (p. 189), or sometimes merely increased secretion of urine — diabetes insipidus (Bernard). The supposition which was formerly held that this

was due to irritation (or, according to others, to paralysis) of a centre for the nerves regulating the formation of sugar in the liver, and which was connected with the vagus, is rendered doubtful in consequence of the altered views of physiologists concerning the processes occurring in the liver (p. 187). Many suppose, as is elsewhere recorded, that it is due to injuries inflicted upon the vaso-motor centre in this region of such a nature as to cause dilatation of the vessels of the liver, kidneys, &c.

The other functions of the medulla oblongata are not well understood, with the exception of those concerned in the reflex actions already mentioned, in which the lower cranial nerves play a part, as, for example, in the reflex operations in the production of saliva (p. 96). The use of the olivary bodies is entirely enigmatical. The crossing of the fibrous tracts in the medulla, as well as certain kinds of involuntary movements which follow injuries to it, will be discussed below.

B. Ganglia at the Base of the Brain, and White Substance of the Brain.

The region between the medulla oblongata and the surface of the cerebral hemispheres contains a number of extensive grey masses—the ganglia already enumerated—and a highly complicated system of white fibres, the general distribution of which has also been given.

In the lower vertebrates, *e.g.* in frogs, it may be shown that, after the power of conscious action has been abolished by removal of the cerebral hemispheres, the possibility of a number of complicated movements still remains, but that these cease when the other parts of the encephalon situated above the medulla are removed. The animals experimented upon are, more particularly, enabled to maintain their equilibrium under varying conditions, and (for example) to prevent themselves, by properly adapted movements, from slipping down a plane the inclination of which to the horizontal is gradually increased (Goltz). Moreover, in these regions, in frogs chiefly in the optic lobes which correspond to the corpora quadrigemina and thalami optici, are situated the arrangements whereby the reflex

powers of the spinal cord are inhibited (Setschenow). The ganglia at the base of the brain are not only in communication with the grey substance of the cord and medulla, and, through these, with almost all the peripheral organs of the body, but are also connected with the nerves of the higher senses, whereby they are concerned in much more manifold and complicated centripetal excitations than are the simpler reflex apparatuses of the cord; hence it would seem that they are the seat of reflex operations and co-ordinations of correspondingly greater complexity; for the complexity of the efferent or centrifugal impulses to activity must increase with the number of afferent or centripetal stimulations. The importance of this region is apparently still further increased by the fact that, besides possessing the means of bringing about excitations in the subordinate groups of centra which it contains, it has the power of inhibiting reflex action. The above-mentioned power of adjusting equilibrium is probably but one slight indication of the functional powers possessed by these organs. The participation of the higher nerves of sense in those powers will be understood when it is remembered that, in the first place, the objects in the field of vision, as well as the muscular sense of the muscles of the eye, influence powerfully our movements;[1] and that, in the second, the auditory nerve is most probably connected with peripheral apparatuses which serve to explain the position of the head; and to these circumstances may be added the centripetal impressions from the whole skin, and from the muscles, the influence of which upon the posture of the body has already been stated (p. 488).

With the above properties of the portions of the brain now being considered must probably be connected the circumstance that unilateral lesions of them give rise to extremely abnormal movements, '*uncontrollable movements*.' The chief forms of these abnormal movements are : (1) movement forwards at the periphery of a circle—like that of a horse galloping round a

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[1] After observing objects in continual motion, or after rotation of the body, the eyes being kept open, the well-known 'dizziness' supervenes when the eye is again fixed upon objects at rest. The reason of this lies in the fact that during movement the eye has to be rotated in a definite direction in order to remain fixed on a point and that this rotation is afterwards continued by habit when the eye endeavours to become fixed upon a point in repose, thus causing the point to seem to move in the opposite direction (Helmholtz).

ring; (2) rotation about the longitudinal axis of the body, —rolling or wallowing movements; (3) movement of the anterior portion of the body about the fixed posterior portion. They follow injuries to the corpora striata, optic thalami, crus cerebri, pons Varolii, and certain portions of the medulla oblongata and cerebellum. More exact statements as to the form and direction of the movements cannot with certainty be given. Their direction changes, in consequence of the crossing of fibres, according as the plane of the section is more anterior or posterior. The older explanation which assumed the existence of centres for the production of movement in a certain direction which were stimulated by these injuries, is inadmissible, because the movements frequently occur merely as abnormal expressions of an intentional movement, such as of flight. Moreover, lesion of white fibres, viz. of the crura, is sufficient to produce them, and they have been sometimes observed to follow injuries to the cortical portion of the cerebrum. Mere paralysis of individual groups of muscles—for instance, in the case of the first class of abnormal movements previously referred to, of the muscles of the side of the body turned towards the imaginary centre of the circle of movement—is also insufficient to explain the phenomena, for this paralysis frequently does not exist. The most probable explanation is the following: Since movements are directed in accordance with sensory stimulations from without, assisted by a knowledge of the situation of the parts of the body, especially of the head and of the eyeballs, all injuries which lead to false judgments concerning those matters—for example, such as cause misrepresentation as to the position of the head—and even injuries to motor tracts which disturb the innervation of the muscles of the head and eyeball, without leading to corresponding impressions, may produce abnormal movements. As a fact, abnormal carriage of the head frequently occurs during such peculiar involuntary movements. Moreover, in the case of movements directed by purely reflex means without the intervention of the mind, injuries to the conducting paths may, under certain circumstances, result in similar movements. Galvanisation of the head also causes dizziness, which may even give place to movements of the above-mentioned description (Purkinje, Hitzig).

Our knowledge of the special functions of individual ganglia

is exceedingly incomplete. The corpora quadrigemina, which communicate on the one side with the optic nerve and on the other with the nucleus of the motor oculi, may be shown, both anatomically and experimentally, to form an important reflex centre between the retina and the internal and external muscles of the eye. After destruction of these organs, reflex contraction of the pupils ceases; irritation of them produces contraction of the pupil of the opposite side, or, according to others, of both sides (Flourens, Longet, Budge). According to more recent statements (Knoll) the above results are said to occur only when the optic tract is implicated, in which case the corpora quadrigemina would not be a centre for the reflex contraction of the iris. On the contrary, stimulation of the anterior corpus quadrigeminum is asserted to cause dilatation of the pupil of the same side, as long as the cervical sympathetic cord remains intact, and therefore to stimulate the centrum ciliospinale. Stimulation of the anterior corpus quadrigeminum also causes rotation of both eyeballs towards the opposite side (Adamük).

The thalami optici, which also communicate with the opticus, do not admit of experimental investigation without the most extensive injury of other parts of the brain. As lesions of the optic thalami produce the peculiar movements above referred to, it is supposed to be through them that the eye influences co-ordinated movements. Pigeons whose cerebra have been extirpated without injury to the thalami optici follow by movement of the head the direction of a light which is carried round them in a circle (Longet). The intimate connection of the optic thalami with the cortex of the cerebrum indicate, in addition, functions concerned in the conscious perception of visual impressions.

Scarcely any facts, save those of an anatomical nature, are known respecting the corpora striata and lenticular nucleus. These organs, which, like the fibres of the crura proceeding to them, have a proportionate development to the cerebrum in the various classes of animals, probably take a part in the production of conscious sensations and movements, which is, however, quite unknown. Lesions of the lenticular nucleus invariably cause hemiplegia. A species of spasmodic attempt at flight has been recently noticed to follow injuries to the corpora striata (Nothnagel).

Nothing whatever has been discovered with regard to the physiological position and function of the numerous grey tracts of the pons Varolii.[1]

In the mass of white substance extending between the ganglia at the base of the brain and the central grey substance an apparently complete crossing of the fibres from one side to the other takes place. The physiological proof of this lies in the circumstance that pathological changes and injuries situated in one of the cerebral hemispheres are followed by anæsthesia, or paralysis of voluntary motion only in portions of the *opposite* side of the body. Not until the lesion has affected, by pressure, &c., the cranial nerves situated at the base of the brain, do symptoms manifest themselves in portions of the head situated on the *same* side as that of the seat of injury. As to the exact situation where the crossing takes place, the discoveries of anatomists and physiologists do not quite agree. For example, while dissection shows an intercrossing of fibres of the white columns in the anterior white commissure of the cord, unilateral sections of those columns are only followed by paralysis of the same side (Volkmann, von Bezold). The crossed commissural fibres are, therefore, possibly merely co-ordinative in function, like those marked 4 in Fig. 40. Fibres cross over from one side to the other in various situations of the spinal cord : firstly, between the pyramids, where, to judge from the connection with the columns of the spinal cord, both motor and sensory fibres are concerned in the crossing, the former, however, passing over at a lower point; secondly, in the white raphe or white lamina occupying the mesial plane of the medulla, where occurs, especially, the crossing of the connecting columns between the grey nuclei of the cranial nerves and the cerebellum, as well as of the fibres running from the nuclei to the peduncles of the brain ; and, thirdly, in the pons Varolii, about the crossing of the fibres of which but little is known. The crossing is completed in the peduncles of the brain.

The olfactory, optic, and trochlear nerves form very remarkable exceptions to the general rule of the intercrossing of nerves. The olfactory fibres are entirely unilateral. The optic fibres cross *outside* the brain in the *chiasma*. According to

[1] It may be here mentioned that nothing is known of the physiological significance of the pituitary body and pineal gland.

some the crossing is only partial, extending to half the number of fibres; but it has recently been stated, in support of the view of the entire crossing, that section of the optic nerve causes dilatation of the pupil of the same side, while section of the optic tract causes dilatation of that of the opposite side (Knoll). The same author also states that section of the optic nerve completely releases the tonus of the sphincter iridis, so that section of the motor oculi nerve no longer causes dilatation of the pupil; and that, therefore, the tonus of the sphincter muscle must be regarded as of reflex origin. The trochlear nerve crosses the middle line *after* its exit from its nucleus, as well as while within the substance of the brain; if the crossing of the fibres within the brain is complete, the twofold crossing will of course constitute the nerve practically unilateral. The physiological and pathological facts, which might serve to throw light upon this point, are still wanting.

C. Cerebellum.

The cerebellum was formerly, but on insufficient grounds, thought to be the seat of certain psychical functions, as of the sexual instinct (Gall) and certain other voluntary acts. Pathological facts and the results of extirpation seem to indicate that it rather resembles the above-described organs in containing a great co-ordinating centre for orderly movements (Flourens, Longet, R. Wagner). Awkwardness in performing movements, frequent falling, and, in birds, the loss of the power of flight, are consequences of its removal, or of disease in its tissues. The connection of the cerebellum with all the columns of the cord, with the ganglia at the base of the brain, and with the cortex of the cerebrum, but especially its intimate relations with the auditory nerve, also renders the above function to a certain extent plausible. It is possible that the auditory nerve, the influence of which in judging of the position of the head has already been repeatedly mentioned, plays a similar part to that of the optic nerve in the co-ordinating apparatus of the middle brain. Deafness does not follow on removal of the cerebellum. In disease of the cerebellum affecting one side only, the disturbances of movement appear chiefly to concern the opposite side

of the body.　Irritation of the cerebellum causes neither move-
ments nor, as far as can be judged, sensations of pain.

D. Cortex of the Cerebrum.

The cortex of the cerebrum must be regarded as the chief,
if not the exclusive, seat of psychical activity.　The essential
proofs of this are the following : 1.　In the animal series the cere-
brum is found to be more fully developed in comparison with the
mass of the body, and with the encephalon as a whole, in those
classes in which the individuals approach, in mental powers, the
condition of man.　The degree of development is judged of by
the weight of the cerebrum and by the number of gyri or ' con-
volutions,' for an increase in the latter increases the extent of
the superficies, and hence the amount of grey substance.　2.
In cases where the cerebrum is abnormally small from birth
(microcephalus, cretinismus), or where it is diseased (hydro-
cephalus, &c.), there is noticed a corresponding diminution in
the higher mental powers, or idiotcy.　3.　Injuries, compression,
and diseases of the cerebrum are almost always accompanied by
mental disturbance—peculiarity of demeanour, insensibility,
somnolence, or excitement.　4.　Removal of the cerebral hemi-
spheres (which is best accomplished in birds) induces a condition
resembling that of sleep, in which all voluntary movement ceases.
Nevertheless, movements of a reflex nature occur in response to
the stimulation of sense-organs; but they are so regular in the
order of their occurrence that they may be predicted.　When
the cerebrum is removed in slices, a gradual loss of all the
powers of the mind is said to take place (Flourens).

It has been also maintained that the various degrees of mental ability in
man are dependent upon the size, development, and weight of the cerebrum ;
the results obtained by *weighing* are far from supporting this supposition.
The height, breadth, and prominence of the forehead are regulated by
the development of the cerebrum ; and a measure of the prominence is
obtained in the ' facial angle,' or angle formed by the intersection of two
lines, one of which touches the most prominent point of the forehead, and the
symphysis of the two halves of the upper jaw, and the other passes through
the base of the skull. The more acute is this angle, the more nearly the face
resembles the type of that of the lower animals. The relative development
of the cerebral hemispheres is best estimated in animals by comparing them
with the corpora quadrigemina, the size of which has evidently no connection
whatever with the degree of psychical development. The cerebra of Mono-

tremata and Marsupialia amongst mammals are distinguished by the circum-
stance that they want a corpus callosum. Of the sulci the fissure of Sylvius,
which separates inferiorly and laterally the temporal and frontal lobes, is the
most constantly found; in many mammals (in mice, moles, shrews, and bats)
it is the only one present, while in others (in hares, guinea-pigs, beavers, &c.)
a few longitudinal furrows and convolutions are added on to the convex
surface. In dogs the fissure of Sylvius is surrounded by three concentric
furrows, whereby four ‘primary convolutions’ are formed; at the same time
a transverse sulcus occurs in the anterior part of the brain, which runs from
the upper part of the longitudinal fissure, and is called the ‘fissure of Ro-
lando,’ or ‘sulcus cruciatus,’ and which is surrounded by the fourth primary
sulcus. In many mammalian brains, possessed of a great number of convo-
lutions, the primary convolutions are more difficult to make out.

It is impossible here to enter upon the description and nomenclature of
the complicated convolutions of the human brain.

The nature of psychical operations requires discussion here
only in one of its aspects. States of consciousness, or *mental
operations*, which are connected in some unknown way with the
material processes of the encephalic organs, entirely elude defi-
nition, as has already been said in the Introduction. But it is
another question, and one which may engage our attention here,
whether the material processes of those organs form connecting
chains between centripetal and centrifugal excitations—a species
of complicated reflex actions—which are independent of the
states of consciousness, or mental operations, and to which the
latter are attached merely as passive concomitants ; or whether
the latter can actively interfere in the material processes,
and so of themselves produce excitation in an organ. The
first view seems not to be in agreement with the existence
of a *free will;* for it has not yet been determined whether
*the same series of centripetal impressions would not constantly
induce in the same organism exactly the same effects, i.e. would
call forth the same apparently voluntary movements.* The
second view presents the difficulty of requiring the assumption
that a scientifically undefinable process acts upon material par-
ticles which obey physical laws.

An essential difference between psychical processes and
orderly reflex acts lies in the fact that in the latter it is only
centripetal stimulations *acting at the time* which are of effect in
inducing them, while, in the former, centripetal excitations
which have long gone by may also operate. It is therefore
necessary, from the materialistic point of view, to assume the

existence of apparatuses in the mental organs in which centripetal excitations leave behind them a *lasting* change. As to the nature of these changes, there exists no ground whatever for supposition.

On the other hand, we are only entitled to assume the existence of psychical functions in cases where the motor reaction following sensory stimulation may be recognised as the associated effect of an excitation which is passed. The other means of deciding the point, viz. the existence or non-existence of states of consciousness, is impracticable, as, strictly speaking, it is impossible to know whether such states occur or not in foreign organisms. Hence we are not justified in ascribing psychical functions to the spinal cord on account of the purposive reactions of headless animals, or of animals asleep, which were previously referred to; for these actions are evidently merely the result of a momentary stimulus, as is shown by the regularity of their occurrence, and are to be regarded, therefore, as pure reflex actions.

From what has been already stated, a general *schema* of the central nervous system may be constructed: A centre ('the central grey matter of the cord'), having apparently no direct connection with the nerves of the higher senses, provides for the simplest reflex acts, in which, essentially, the organs in the vicinity of the body take a part when excited : this the simplest kind of reflex actions might be described as ' plane reflex acts, or reflex acts in one plane.' A second centre of a higher nature ('ganglia at the base of the brain, cerebellum (?)'), which is connected with all the regions dependent upon the first centre, and in addition with the higher nerves of sense, and which possesses also inhibitory fibres controlling the first-named centre, provides for more complicated actions and reflex actions, in which distant parts of the body are concerned, *e.g.* reactions of the extremities following visual impressions, locomotions which are directed by the eye, &c. A third centre of the highest kind ('cortex of the brain'), which is in connection with the others, has the property, on the application of certain centripetal impressions during the waking state (?), of becoming so changed for considerable periods, or for ever, that unequal complicated actions may result ; for, in addition to the manifold combinations of momentary centripetal impressions, numerous impres-

sions of the past also have a distinct action in centrifugal exci-
tation. The number of the possible combinations is, therefore,
so immensely great that there is ample scope for theory to ex-
plain all actions as the results of centripetal influences. Ex-
citation of this highest centre is accompanied by states of con-
sciousness, and here is the limit of physiological observation.

It is not possible to give more detailed statements as to the
arrangements in the centres of the cortex of the cerebrum. The
entirely gratuitous phrenological division of the *mental func-
tions* according to ' impulses,' and the equally baseless localisa-
tion of them in regions of the cerebral cortex, have long been
recognised as meaningless and false. It is also impossible to
assign any individual spot in the cerebrum as the seat of con-
sciousness, since cases are known, in connection with almost every
part, in which, when that part was destroyed or was wanting,
consciousness still remained. Local defects in the cerebrum
merely separate certain regions of the body situated on the
opposite side from connection with the mind, while conscious-
ness may still remain after destruction of one hemisphere.
Unfortunately, we possess no trustworthy experience as to
whether, after such destruction, any portion of the images im-
pressed on the memory have been effaced, or as to the connec-
tion which exists eventually between the place of injury and the
loss of memory.

Unilateral injuries, induced by rupture of the white sub-
stance of either hemisphere indicate that the mind communi-
cates with the various regions of the body by means of definite
fibres. The question now arises, Do these groups of fibres
spring from definite regions of the cerebral cortex, or from
diverse regions, or even from all portions? The first of these
possibilities seems to be supported by the circumstances that
pathological changes affecting a certain anterior portion of the
brain, namely, the *Island of Reil* (which is situated at the
bottom of the Sylvian fissure, and which is discovered projecting
downwards between the two branches of the fissure), as well as
lesions of the grey lamina of the *claustrum* which is situated
between the *Island* and the lenticular nucleus, induce a condition
called ' Aphasia,' in which the patient is unable to speak words
while retaining the power of writing them. The knowledge
derived from experiment concerning the individual sensory and

motor functions of the cortex is in the highest degree indefinite. Mechanical lesions occasion, according to most authors, neither pain nor movements. The movements which have recently been induced (Fritsch and Hitzig, Ferrier) by electrical stimulation, since they do not occur after mechanical or chemical stimulation, may very well be set down to the irritation of more deeply seated regions, for the latter are unavoidably exposed to the diffusion of currents. This explanation is especially probable in the case of Ferrier's experiments. According to the results obtained by the observers just mentioned, the anterior parts of the cerebral cortex in particular are connected with the motor arrangements. Experiments with destruction of small parts of the cortex by excision (Fritsch and Hitzig), or by cauterisation by means of injections into the tissue (Nothnagel, Fournié), resulted for the most part in abnormal postures and movements of individual members, which are attributed (Nothnagel) to loss of muscular sense. No results as to the nature and distribution of the functions of the cortex, even of the value of approximations, can be deduced from these experiments.

Most cases of the above-mentioned ' Aphasia' depend upon lesions of the *left* hemisphere, and are accompanied by paralysis of the *right* half of the trunk (*right-sided hemiplegia*). It has therefore been concluded, not without opposition, that the so-called 'centre of speech ' is unsymmetrical —unilateral. Cases are, however, known of Aphasia following lesion on the right side (Bouillaud), and the greater frequency of the former kind is referred to circulatory agencies.

The results of electrical stimulation of the cortex are the following (Fritsch and Hitzig): Within the arch circumscribed by the four primary convolutions and the sulcus cruciatus (in the dog) is situated, in the anterior region, a spot the irritation of which induces contraction of the cervical muscles; in the lateral region a similar spot exists for the extensors and adductors, and a little way behind is another for the flexors and rotators of the fore limb, while a fourth for the muscles of the hind limb is found at the posterior part of the space. At the posterior part of the convolution which surrounds the fourth, is found a spot for the muscles supplied by the facial nerve. In spite of the close approximation of the electrodes one to the other, it is impossible to prevent a diversion of the current through the deeper portions of the brain. This surmise is not out of harmony with the fact that slight changes of the position of the electrodes induce changes in the results, for the direction of the diverted currents is very much altered as the electrodes are shifted even over small areas.

We must not omit to mention that there exists in rabbits, in the neighbourhood of the posterior apex of the hemisphere, a spot on injuring which violent but transitory forward and sideward movements result after

some time (Nothnagel). In this case it would seem that the movements were due to some hallucination on the part of the animal rather than to a direct motor influence.

Direct combinations of the cerebral cortex with sensory or motor nerve-fibres of the external system are rendered doubtful on the anatomical grounds above mentioned, and at most only occur in special regions. It seems more probable that the same apparatuses are made use of in the production of conscious sensation and voluntary movement as in the production of reflex acts of a lower or a higher order. As in the latter motor nerve-centres are so combined that the muscles co-operate in orderly manner to cause reflex action, so it is possible that in orderly voluntary movements also these co-ordinating systems are brought into activity *as a whole*, whereby the mind is, as it were, spared much labour. This is rendered all the more probable as we cannot voluntarily contract each individual muscle alone. It is probable that the mental organs are provided not only with inciting fibres, but also with inhibitory fibres, for these centres. Whether intermediate apparatuses, concerned in similar influences exerted on the organs of the mind, are present in the case of centripetal excitations also, is still more doubtful, and such would, at least, be far less intelligible.

In addition to the above-described purposive co-ordinations of movements, there exist others, which might be described as defects or weaknesses; in contradistinction to 'co-ordinated,' these are called 'associated' movements, to the category of which belongs, *e.g.*, the wrinkling of the skin of the forehead during strong bodily (or mental) excitement. It is possible to render oneself, by an act of will, temporarily and, by frequent repetition, permanently, free from these 'movements of association,' as is shown in the independence of the two hands of a pianist.

Sensations in the region of other fibres than those which have been objectively excited are called 'associated sensations.' One illustration has already previously been given (p. 464), viz. the phenomenon of 'Irradiation,' or the apparent implication in stimulation of regions which were not themselves excited, in the neighbourhood of an excited cutaneous nerve-fibre, which is owing to the various connections of the grey substance of the cord. In other cases remote fibres also may appear to the mind to have been stimulated, probably because of the closeness of the stimulated and the

non-stimulated fibres at their origin in the grey substance; for example, the sensation of tickling in the larynx which follows when the external auditory meatus is touched near the tympanum, both regions being supplied by the vagus. 'Irradiation' also may be diminished by practice, as shown by the more acute perception of the touch (due to the diminution of the areas of sensation) in blind persons.

By means of the method described on p. 336, and similar contrivances, the rapidity of certain simple psychical processes may be determined. In these experiments (Donders, De Jaagrr) it appeared that a signal prearranged to be given on a certain stimulation occurred later, the more complicated the psychical operation which was necessary for the production of the signal, and that, in addition, the time varied according to the way in which the stimulus acted. For example, as a means of experiments, (1) the time which elapsed between a cutaneous stimulus, and the giving of a signal, which had to be varied by the person experimented upon according as the one or the other of two localities of the skin had been stimulated (*i.e.* decision had first to be made as to which of the localities had received the stimulus) was 0·066 sec.; (2) when light was used as a stimulus, *a*, decision between two colours took 0·122—0·184 sec., *b*, decision between two letters of the alphabet took 0·166 sec., *c*, decision between five letters took 0·170 sec., the signal consisting in pronouncing the name of the letter which was suddenly exhibited; (3) when the stimulus was auditory, *a*, distinguishing between two vowels took 0·056 sec., *b*, distinguishing between five vowels took 0·069—0·088 sec., the signal consisting in repeating the name of the vowel.

If objects be allowed to act upon the eye for only a very short time, they are not recognised; the time during which the eye must be stimulated in order to ensure recognition is, for large letters, about 0·0005 sec., and it is longer the smaller the object and the less it differs from the ground on which it rests. If a second object is presented to the eye immediately on the disappearance of the first, the first must be observed for a longer time in order to be recognised, and the longer according as the second object is a more powerful stimulus, and as the first object is more complicated in form (Helmholtz and Baxt). If, prior to the momentary illumination of an object, the attention be directed to a certain part of it, that part is perceived even though, without having the attention so directed, the illumination would be of too short duration for it to be possible (Helmholtz).

Psycho-Physical Relations.

As it is impossible to define the nature of states of consciousness, there exists, of course, no measure for them. Nevertheless in recent times, in the more exact consideration of those states of consciousness which are most accessible to investigation, viz. the sensations, a method of measurement has, by an artifice, been introduced. By this method a definite relationship appears

to have been established between the increase of the state of exci-
tation of the mental organ and the increase of the state of con-
sciousness (sensation). It must not be overlooked, however,
that between the material process in the organ of sense and that
in the organs of mind there intervenes a whole series of *libera-*
tions, concerning the relations of which nothing is yet known;
we are, therefore, entirely ignorant as to where to localise this
relationship, which has been termed ' psycho-physical' (Fechner).

These psycho-physical discoveries were made by determining
the slightest increase of stimulus which was perceptible as a
sensation, *i.e.* the increase of stimulus which occasioned the
smallest possible increase of sensation. The increase of stimulus
is within certain limits *constantly proportional to the strength*
of stimulus already applied (E. H. Weber), *i.e.* ' the stronger
the stimulus (as, for instance, a pressure) already in action, the
more must it be increased, in order that the increase may be
perceived.' This law holds true in the case of all the organs of
sense (Fechner, Volkmann). It follows therefrom that *sen-*
sations increase proportionately to the logarithms of the
strength of the stimulus (Fechner).

If β represent a stimulus, γ the sensation which corresponds to it, $d\gamma$ the
smallest perceptible increase of sensation, and $d\beta$ the increase of stimulus
necessary to produce that increase of sensation, then, according to Weber's
law, $d\gamma$ is not proportional to the absolute increase of stimulus $d\beta$, but to the
relative increase of stimulus, measured according to the strength of stimulus
β, *i.e.* to $\dfrac{d\beta}{\beta}$. Therefore if k be a constant

$$d\gamma = \frac{k \cdot d\beta}{\beta} \,.$$

If this equation be integrated, the sensation γ being considered as a sum
of numerous small increases of sensation, then

$$\gamma = k \cdot \log. \text{ nat. } \beta + \text{const.}$$

If the constant of integration be so chosen that when $\gamma = 0$ β is equal to b
—that is to say, if b is the intensity which the stimulus must already have in
order to be perceived ('initial' or 'liminal' intensity, 'Schwellenwerth' of
Fechner)—then

$$\gamma = k \ (\log. \ \beta - \log. \ b) = k \cdot \log. \ \frac{\beta}{b} \,,$$

which expresses that γ commences to be positive when $\beta > b$. The formula
for γ (the ' Maassformel' of Fechner), which becomes valid for every lo-
garithmic system by changing the value of k, therefore, shows that sensations
increase with the logarithm of the stimulus (considered in relation to the
' liminal intensity '), and shows that, in general, with increasing stimuli the

sensations (corresponding to the logarithms) increase, at first quickly, and then more and more slowly.

The resistance which was (p. 480) assumed to be offered by the grey network of the spinal cord, and the magnitude of which determines the extent of the circle of irradiation (p. 464), may, with the aid of certain hypotheses, serve as the starting-point of another deduction from Fechner's formula.

If it be assumed (1) that the resistance is so constituted that in being propagated the excitation is constantly diminished by an equal fraction of its own value; (2) that the imperceptible value which it finally attains is equal to the *liminal intensity* of the stimulus; and (3) that the intensity of the sensation is proportionate to the magnitude of the area of the circle of irradiation,—the same relation between strength of stimulus, liminal intensity, and intensity of sensation is found as is expressed by 'Fechner's formula' (Maassformel). On the other hand, the empirical determination of the 'formula of intensity' may, by Weber's law, serve for the verification of the above assumptions. It is thus at once found that k in the formula of intensity is inversely proportional to the central resistance (Bernstein).

It is impossible to enter here upon the further simplification and application of 'Fechner's formula' to special cases. As regards the ' *liminal* intensity' of the stimulus it may, however, be remarked that, since the effect of a stimulus depends on many circumstances (intensity, duration, distribution over many or few sensitive elements, suddenness of action, &c.), the 'liminal intensity' also may be represented in various ways. The stimulus of a musical *tone,* for instance, may be considered as the product of the number and of the intensity of the component vibratory stimuli, so that the 'liminal intensity' of a high tone will correspond to a smaller degree of intensity than the 'liminal intensity' of a low tone.

Sleep.

In the mental organs two states, the physical difference between which is not understood, hold alternate sway with a certain regularity; these are the waking and the sleeping states.

There appears to be a kind of sleep in which no mental action whatever takes place, so that the only central organs in operation are those of an automatic and reflex nature. The functions depending upon the central organs of this character, viz. circulation, respiration, secretion, digestion, &c., go on as usual. The reactions to external stimuli which still manifest themselves, and which proceed exactly like those of animals whose cerebra have been extirpated, must be regarded simply as undisturbed orderly reflex movements; for, as was explained on p. 512, we have no grounds for regarding them as the results of still remaining mental activity, having its seat either in the cerebrum or perhaps in special mental organs (as of the spinal cord, &c.) not in the sleeping state.

Whether states of consciousness or mental operations occur during sleep can only be decided by one means, that of the memory. From it we learn that incomplete mental actions do very frequently take place in the form of *dreams*. These are marked by sensations without objective causes (hallucinations), volitions without effect (disappointments in intended but impossible movements), and processes of thought without the usual logic of the waking state (apparent solutions of problems which seem afterwards when remembered to be absurd). No means exist of determining the duration of dreams. An observation which has frequently been made leads to the belief that possibly most dreams occur only at the moment of awakening or, at least, at the moment of a sudden and momentary release from sleep; for a dream often ends with a sensation occasioned by some objective cause which, at the same time, brings about the awaking of the sleeper. Hence the fact that extraordinary delusions as to time are an accompaniment of dreams.

Awaking from sleep appears for the most part to be caused by sensations which must be stronger the deeper the sleep. The depth of sleep may be expressed by Fechner's formula given above, by making the liminal intensity b (*i.e.* the value which a stimulus must have in order to induce a state of consciousness) so great that γ becomes negative on ordinary stimulations. Direct measurements have shown (Kohlschütter) that b, and consequently the intensity of sleep, increases from the commencement of sleep, at first quickly, then more slowly, until about the end of the first hour, after which it again

diminishes, at first quickly and then very slowly, reaching its usual value at awaking-time. Frequently, and without any apparent cause, sleep becomes suddenly less intense, relapsing again to its former depth. As a general statement, the deeper the sleep the longer it lasts. The deeper the sleep, and the greater, therefore, is b, the stronger must the stimulus β be which is requisite to call forth a sensation and cause awaking.

The chief condition of sleep is the removal as far as possible of all stimuli: hence the stillness and darkness of night are conducive to sleep. Sleep, moreover, seems to come more readily and to be deeper the greater the preceding exertions of the mental organs. During sleep the mental organs are restored to vigour, and the exhausted muscles, which are for the most part relaxed during its continuance, become refreshed. The numerous and well-known phenomena of sleep and dreaming may be passed over without further comment. Concerning the material changes in the brain during sleep, the alterations of blood-pressure, nutrition, &c., we have as yet mere hypothesis unsupported by facts.

APPENDIX. *Circulatory and Nutritive Conditions of the Brain and Spinal Cord.*—The activity of the central organs is dependent in a high degree upon their blood-circulation, as the consequences of anæmia, hyperæmia, stagnation, &c., show (p. 501). Special arrangements appear to exist with a view to regulate the blood-pressure. As such may be mentioned: 1. The fact that brain and spinal cord are enclosed in a bony case which they, together with the cerebro-spinal fluid, completely fill. On account of the incompressibility of these parts, and of the unyielding nature of the enclosing case, cardiac and respiratory variations in the vascular areas appear to be impossible. In order that such variations should occur, either the case must be opened (thus, the brain shows respiratory pulsations when the skull is opened; and a manometer communicating with the interior of the cranium exhibits respiratory and cardiac oscillations) or the cerebro-spinal fluid must flow out (thus, in injuries to the spine, the brain shows respiratory movements which, as it seems, induce basilar meningitis by friction, Rosenthal). Artificial or pathological increase of intracranial pressure causes much disturbance of function, presumably depending upon circulatory mischief. 2. The brain, by means of the circle of Willis, is secure from any sudden interruption to circulation by the closure of an artery. 3. Changes of blood-pressure in the brain, which might result from sudden changes in the position of the body (as, for instance, on rising from the horizontal position), are said to be prevented by the thyroid body which forms a collateral blood-reservoir (Liebermeister). If the change of position occurs suddenly a transitory faintness follows. The thyroid body is said to ulate blood-pressure in the brain in another way also, since, when

swollen by the strong influx of arterial blood, it compresses the carotid (Guyon); that is to say, when the muscles are powerfully excited, the carotids sometimes exhibit no pulsation (Maignien). 4. The vaso-motor nerves of the brain, which traverse the highest cervical ganglion, but do not wholly lie in the sympathetic cord (Nothnagel), are the media for the general regulatory influences such as are described at p. 79.

3. Sympathetic Centres and Nerves.

In general those nerves are described as sympathetic, irrespective of their origin, which supply the viscera and the vessels. Moreover, the non-medullated nerve-fibres, which are present in such large numbers in sympathetic nerves, are called 'sympathetic fibres.' The origin of these sympathetic fibres is not exactly determined. The numerous ganglion-cells which are aggregated in the large somatic cavities, or are scattered singly through the parenchymata of many viscera, are to be regarded as the principal central organs of the sympathetic system ; but it has been shown anatomically and physiologically that many sympathetic fibres are in communication with the cerebro-spinal organs, partly by means of the rami communicantes of the spinal nerves, and partly by means of unions formed with the cranial nerves. This communication has been already alluded to in the description of the oculo-spinal centre (pp. 489, 507) and of the origin of the vaso-motor nerves (p. 502). Nevertheless no sympathetic nerve has ever been proved to be in connection with the will, for all the movements of the viscera are completely *involuntary.* The sensibility of the viscera, also, is so extremely slight that it is supposed to be due to the few medullated ('cerebro-spinal') fibres which the sympathetic nerve-trunks contain. Smooth muscles are regulated only by sympathetic fibres, and hardly any instance is known of other descriptions of muscles being supplied from this system of nerves.

The ganglion-cells of the sympathetic and spinal ganglia are surrounded by a capsule covered with squamous epithelium (Fräntzel). They give off, as a rule, a straight fibre, and a spiral one which twists round the former (Arnold, Beale) ; hence they are to be regarded as bipolar. It is, however, stated that, in the spinal ganglia, only unipolar cells are found (Courvoisier, Schwalbe).

The functions of the sympathetic central organs are, as far

as is known, the following: 1. To subserve reflex action, which, so far as muscular movements are concerned, is of the purposelike, orderly character previously described (p. 477); hence co-ordinating arrangements must exist in connection with them. In addition to motor reflex actions we get also secretory. 2. To subserve automatism (motor and secretory). Possibly many of these apparently automatic excitations ought to be classed as reflex: the cerebro-spinal organs cannot be concerned in such excitations, as the functions ('vegetative') which really depend upon the sympathetic system continue for a long time after destruction of these organs (Bidder). In the case of automatic, as of reflex, actions co-ordinating arrangements are recognisable. The rhythmical automatism in sympathetic nerves is under the regulation of inhibitory and accelerating fibres, just as was the case with nerves of the cerebro-spinal system (p. 472).

The following may be taken as a more particular statement of the functions of the sympathetic organs:—

1. *The Ganglia of Parenchymata.* Many organs contain in their substance ganglion-cells, by means of which their functions are in part regulated. Such organs are especially the heart, and, according to most authors, the stomach, intestines, uterus, &c. The ganglia of the heart are most easily studied. They possess a rhythmical automatism in virtue of which isolated fragments of the heart pulsate of themselves. In addition, co-ordinating arrangements are present whereby the various segments of the isolated and uninjured viscus contract in regular sequence. Moreover, the rhythm is under the control of accelerating and retarding fibres, both of which sets arise from the cerebro-spinal organs, but the former of which run in sympathetic courses (viz. through the lowest cervical and uppermost thoracic ganglia), while the latter pass along the vagus. The customary assumption that the heart also contains (in the auricle) *inhibitory central organs* is doubtful.

The stimulus which produces automatic excitation of the cardiac ganglia is unknown. In the frog's heart it appears to be the oxygen of the air or of the blood, since regular pulsation ceases on excluding the oxygen (Goltz, Cyon), although direct stimulation still induces contraction, the muscles themselves, therefore, remaining irritable. On the other hand, the presence of carbonic acid appears to excite the inhibitory system (Traube, Cyon). In the

case of mammals the conditions are more difficult to grasp, as it is impossible to experiment with the isolated heart.

Intestinal peristaltis affords another example of automatic co-ordinated movement brought about by parenchymatous ganglia. · In this case also an inhibitory mechanism (for the small intestine) is found in the splanchnic nerves, while it would seem that accelerating fibres reach the intestine from the sympathetic plexuses of the abdomen. The stimulus for this automatism is also unknown.

The presence of air increases the movements, as does also an increased venous condition of the blood, caused, for example, locally by stagnation (p. 148).

Concerning the innervation of the uterus Chap. XII. may be consulted. •

2. *Ganglia, Plexuses, and Sympathetic Cord.* Nothing is known about the action of the numerous ganglion-cells found in these structures. Experiments in which stimulation and section have been made use of have merely led to a knowledge of the fibres, derived apparently from the cerebro-spinal organs which chanced to pass through them. The only apparently established fact indicating the existence of reflex powers in a ganglion, viz. the secretion of saliva induced in a reflex manner through the submaxillary ganglion (p. 96), has recently been doubted (Eckhard); for the result follows on electrical stimulation only, and may be due to a diffusion of the current, which may thus affect the secreting nerves themselves.

In the cervical portion of the sympathetic the following fibres have been shown to exist :—

1. Vaso-motor fibres for the corresponding half of the head : these have their origin in the cerebro-spinal organ.

2. Fibres for the dilatator pupillæ : these also take origin in the cerebro-spinal organ.

3. Fibres for the smooth orbital muscle of Müller, and also, apparently, for the rectus externus muscle, since section of the cervical sympathetic induces internal strabismus.

4. Secreting fibres for the salivary glands, and for the lachrymal glands : the origin of these is unknown.

5. Accelerating fibres for the heart (von Bezold).

6. The lowest cervical ganglion, besides the highest thoracic

ganglion *(ganglion stellatum)*, with which it is frequently united, conducts accelerating fibres to the heart through the third branch of the ganglion (E. and M. Cyon); the first and second branches are the roots of the depressor nerve.

7. Fibres proceeding to the cerebro-spinal organ which call into activity the cardiac inhibitory mechanism.

8. Fibres proceeding to the cerebro-spinal organ, which stimulate the vaso-motor centre (pressor fibres).

In the thoracic portion of the sympathetic but few clearly established experimental results have been obtained. The superior thoracic ganglion *(ganglion stellatum)* conducts to the heart accelerating fibres, which reach the ganglion by way of the cervical sympathetic cord (von Bezold) and the root accompanying the vertebral artery (von Bezold and Bever).

The plexus cardiacus, belonging to this part of the sympathetic system, is constituted of fibres passing to and from the heart and belonging to the vagus, depressor, and sympathetic nerves. In the thoracic portion also arise the splanchnics, major and minor, to which the following fibres may be assigned (spl. major): 1. Inhibitory fibres for the intestine (p. 148). 2. Accelerating fibres for the intestine (surmised from the effect of post-mortem stimulation, p. 148). 3. Fibres inhibiting the renal secretion. 4. Vaso-motor fibres for the extensive vascular region of the abdomen. 5. Centripetal fibres which inhibit the heart in a reflex manner (situated in the frog in the sympathetic cord (Bernstein). 6. Fibres, irritation of which causes an abnormal appearance of sugar in the urine (von Gräfe, Eckhard, Ploch).

Concerning the abdominal portion of the sympathetic we have but few trustworthy statements. Irritation of the cord and the plexuses (cœliac, mesenteric, renal, suprarenal, spermatic, hypogastric) causes for the most part movements, or increased movements, of neighbouring organs, viz. intestine, bladder, ureters, uterus, vesiculæ seminales, and spleen (induced, in the last-mentioned organ, by irritation of the plexus lienalis, a branch of the cœliac plexus, Jaschkowitz). Section or extirpation of the sympathetic cord and plexuses cause chiefly circulatory and nutritive disturbance. It may be mentioned that extirpation of the cœliac ganglia produced, in one well-

established case, a disturbance of digestion, in which undigested food was voided *per anum* (Lamansky).

The discoveries which have been made concerning the uterus will be given in Chap. XII., when considering parturition.

The suprarenal capsules are very rich in nerves and contain in their interior cells resembling ganglion-cells; on this account their function has been supposed to be nervous, but this is as yet unsupported by facts. Other suppositions as to their nature have already been stated on p. 178.

PART IV.

ORIGIN, DEVELOPMENT, AND DEATH OF THE ORGANISM.

CHAPTER XII.

A. GENERAL OBSERVATIONS.

THE origin of new organisms is always associated with the existence of others which have preceded them. Since the belief in the free formation of cells has been almost universally abandoned, one may affirm that no organic form originates in shapeless matter, but that each form is derived from a pre-existing one. The general plan of new formation is either a decomposition of an organism into parts which henceforward develop independently, or the separation of a part which develops individually from an older organism which continues to exist; the new part may either remain in connection with the old or may separate from it.

The doctrine of *spontaneous* or *equivocal generation*, which ever finds defenders—the doctrine which affirms that organised beings do spring from shapeless matter, as in fermenting or decomposing fluids—is opposed to the statements made above.

The apparent proofs of such spontaneous generations are :—

1. The development of vegetable and animal organisms (fungi, infusoria) in infusions of organic substances.

2. The development of organisms (entozoa) within completely shut cavities. In both cases, however, the organisms spring, as may be proved, from the numerous germs contained in the air; as the infusion remains barren if the air reach it without any germs (these being separated by filtration from it), or if the germs contained in the air be destroyed before

it reaches the infusion, as by conducting the air through red-hot tubes. The development of entozoa is unquestionably due to the germs which are introduced with the nutriment, and which can in certain stages of their existence wander into the closed cavities of the body.

Notwithstanding what has been said in opposition to the present occurrence of spontaneous generation, science teaches us that the temperature of our globe was once so high that no organised being can have existed upon it, so that at some period in its history a true primordial generation must have taken place.

The resemblance between the parent organism and its offspring not only extends to the general form, but to peculiarities of formation, which characterize not merely *the genus*, or the *species*, but even the *variety* or *race* to which it belongs, so that peculiarities in form which have arisen accidentally can easily be transmitted.

This constitutes the basis of the attempt to explain the origin of species and genera through inherited and ever increasing varieties in form (Darwin). In order to explain the fact that a variety in form, once present, develops further and further, an assumption suffices, upon which the Darwinian theory is based, viz. that of all existing organisms only a fraction meets with the conditions necessary to continued existence, and that consequently a struggle for existence is going on amongst living beings. In this struggle those beings will always be the conquerors which are endowed with properties which render them adapted to the local conditions in which they are placed. If, therefore, in any animal species a certain variety of form has arisen, which renders the individuals concerned more suited to the existing conditions than their fellows (as, *e.g.*, more able to procure nourishment, to bear particular temperatures, to vanquish foes, to allure the opposite sex for purposes of reproduction), then these individuals will, under the given circumstances, hold the upper hand in the struggle for existence, their peculiarities will be maintained by inheritance, and by further variation in the same direction will establish a wider and wider separation from the original form. In this way it is possible that from the same stock there may be developed in different localities such deviations that out of varieties there may spring new species, and out of species new genera.

The inability to discover the transition-forms between two species is easily seen to depend upon the fact that, of all the forms which result from one stem, the extreme forms least of all come into collision in the struggle for existence, whilst the mean forms most easily are destroyed in the process.

By carrying the same principle further, but in an opposite direction, the surmise is formed that all animal (and vegetable) forms spring but from a few, perhaps even from a single parent form. The Darwinian hypothesis has, also, another fruitful side, in that it destroys specially all teleological speculations, by showing that of all possible forms which can exist, only those most adapted to their uses can survive, whilst the others must succumb.

Seeing that in the breeding of animals the hereditability of certain peculiarities is taken advantage of, and these peculiarities are thereby further developed, the individuals which possess them in a pre-eminent

degree being specially cared for and employed in propagation, the principle above alluded to has by its expositor been denominated '*natural* selection.'

Forms of Reproduction.

The fundamental forms of reproduction are the following :—

1. Fission of the existing organism into several pieces (of equal value), which continue to live independently, either united or separated, and which grow to the size of the original organism. This is spoken of as the *fissiparous* mode of reproduction. Closely connected to this is the separate continued existence of the pieces of animals which have been artificially divided, and which has often been observed.

2. Scission of a constituent part of the parent organism. The constituent part may either remain joined to the parent or may separate from it ; in either case it develops independently of it, whilst the parent continues to exist. If the part which separates is an important multicellular constituent of the parent organism which remains united with it for a time or for ever, the process is termed '*gemmiparous* re-production.' If, however, the separating portion be but a single cell, which develops independently of any connection with the parent organism, the process is termed '*oviparous* reproduction,' and the cell concerned in this process is called 'germ-cell,' or 'egg,' or 'ovum.'

The fissiparous and gemmiparous modes of reproduction only occur in the lowest animal forms. The oviparous mode, on the contrary, occurs throughout the rest of the animal kingdom, even in man, and in many of the lower animals in addition to the first-named processes of reproduction.

The ovum is the product of a special organ, 'the ovary.' It is only in a few animals that the development of the egg proceeds alone to the very end ('*parthenogenesis*').

In order that development may occur, or at any rate proceed beyond a certain limit, the egg requires, as a rule, contact with a peculiar element. The peculiar element is '*semen*,' the product of another organ, the 'testicle.' The ovary and the testicle are either (as in the higher animals) found in separate individuals or they are both present in the same individual. In the first case the individual furnished with the ovary is termed *female*, as distinguished from the *male*, which is provided

with the testicle; in the second case the creature (as in many of the lower animal forms) is said to be 'hermaphrodite.' The contact of semen and ovum is called 'fertilisation' or 'impregnation,' and reproduction by means of eggs which have to be fertilised is spoken of as 'sexual reproduction;' the fissiparous and gemmiparous modes of reproduction, as well as parthenogenesis, constitute, on the other hand, 'non-sexual' modes of reproduction.

Undoubtedly parthenogenesis has, hitherto, only been certainly determined to occur in a few species, and in them it only occurs side by side with true sexual reproduction, and yields invariably only individuals of one sex (*e.g.* in bees and in a species of wasp, only males, in the *psychidæ* females).

The best known example, that of bees, may here be specially considered. In a bee-hive there occur three classes of individuals, viz. males (which are called *the drones*), females incapable of reproduction (*the working bees*), and one female capable of reproducing (*the queen bee*). The queen bee once in the year, in what may be termed the nuptial flight, is impregnated by one of the drones which surround her, and returns with a full 'receptaculum seminis.' She is now in a position either to fertilise the eggs which she lays or to leave them unfertilised. Both these events occur, and they are governed by the cell in which the egg is deposited; in the cells of the drones are placed the non-fertilised, and in the cells of the working bees the fertilised eggs. The emission or non-emission of the semen which is stored up depends either upon the will (instinct) of the queen bee or upon the mechanical relations of the cell into which she thrusts the posterior part of her body.

Whether the fertilised ovum develops into a sterile female (working bee) or into a fully developed female (queen bee) depends upon the feeding of the larvæ by the working bees, perhaps also upon the form and size of the cells.

A momentary parthenogenetic development occurs in some animals, in which the non-fertilised egg goes through the early stages of development (first stages of cleavage), and then an arrest occurs; such a process has hitherto been observed in the sow (Bischoff), in the rabbit (Hensen), and in the hen (Oellacher).

Sexual Maturity. Fertility.

In the case of all organisms the conditions required for reproduction first occur at a particular stage of their development, generally only when their growth is completed, so that the excess of 'the receipts' over 'the expenditure' of the body which has hitherto served the purposes of growth may thenceforward be used in the production of generative materials, or

even (in the case of viviparous creatures) in the nutrition of the developing egg. It is only at this particular period (period of puberty) that in animals of different sexes the complete development of the germ-preparing organs (ovary and testicle) occurs. Henceforward, however, for long periods of time, often until death, the reproductive process proceeds, generally at regular intervals. The number of the progeny of one individual, or of one pair of individuals, *i.e.* their 'fertility,' varies very greatly throughout the animal kingdom. In making such a quantitative determination one may start from two different stand-points. If reproduction be looked upon as a function of the maternal organism in relation to other functions, viz. as an expenditure in relation with the other sources of expenditure and income which constitute the whole exchanges of the matter of the body, then we must determine the relation between the weight of the animal and the weight of the reproductive material yielded by it in the condition in which it leaves the body (as eggs in the oviparous, young creatures in the viviparous, semen in male animals). Such determinations (Leuckart) exhibit enormous differences in the expenditure of. generative matters; thus, for example, the yearly generative expenditure of the female organism is, in the human female, about $\frac{1}{14}$ of the body weight, in the sow about $\frac{1}{2}$, in the mouse about three times the body weight, in the hen five times, and in the queen bee 110 times the body weight. If now we consider reproduction in relation to the maintenance of the species, we must compare, instead of the weight, the number of the real progeny resulting. The first kind of determination alluded to cannot be utilised for this purpose, for, firstly, the same weight of generative material represents in different species a widely differing number of *possible individuals*; and, secondly, a great number of circumstances must concur in order that fertilisation and development should occur, and these circumstances are relatively only rarely present, so that in general only a small fractional part of the generative material really accomplishes its end.

The number of the progeny can, however, only be very rarely determined; as one may, however, venture to assume that the object of reproduction is to maintain the number of individuals of the species approximately constant, it follows that the

number of the progeny stands in a certain relation to the mean duration of life of the species. If we designate the number of years of the latter by n, the constant number of individuals by a, the number of individuals which must be born in a year will be $\dfrac{a}{n}$. For each individual being of the species, there will be yearly born in the mean $\dfrac{1}{n}$ of progeny. How much of this production falls upon each reproductive individual depends principally on, 1, whether the new creature originates sexually, *i.e.* by the concurrence of two parents; 2, the number of reproducing individuals in relation to the total number, as well as the duration of the period of fecundity in relation to the duration of life. The number of germs produced will, in general, exceed the numbers obtained by the above methods, the rarer are the conditions realised necessary for fertilisation and development.

Sexual Reproduction.

The egg (ovum) in its simplest form is a globular cell, the granular lecithin-containing protoplasm of which is called the yolk (vitellus). Besides this, many eggs possess a (secondly deposited) secondary yolk (Nebendotter), which occasionally consists of immigrated cells. The vesicular nucleus of the ovum is called the *germinal vesicle* (vesicula germinativa), and the nucleolus which is seen in the vesicle is called the *germinal spot* (macula germinativa). In many eggs a cell-membrane cannot distinctly be made out, and in the majority of cases the cell is found surrounded by an envelope of different form and not belonging to it, which, when a vitelline membrane is present, is deposited upon it. This envelope is in its simplest form a structureless, tolerably thick, membrane, so that seen in profile it appears as a bright ring (zona pellucida of mammalia and man). In the majority of eggs it is perforated by numerous canals; in some it is covered by villus-like processes, the most diverse forms being observed in invertebrate animals. In many animals the envelope possesses a tolerably large opening, which is of importance in the process of fertilisation, and which is called 'the micropyle' (Keber); this is especially the case in

numerous invertebrata and fishes, probably also in higher verte-
brata.

The chemical constituents of the yolk of the egg are princi-
pally derivations of lecithin (vitellin, ichthin, protagon (?), see
p. 36), various albuminous bodies, a colouring matter related to
hæmatoidin (p. 28), an amylaceous body, salts and water.

In many cases the egg possesses accessory envelopes, which it partly
brings with it from the seat of its formation in the ovary (as the *discus
proligerus;* the yellow of the bird's egg is to be looked upon as the en-
tire ovarian follicle, and only the germ-disc is the ovum proper), partly
it receives on its way through the excretory passages; thus the white
and the shell of the bird's egg are formed around it in its passage through
the oviduct—a passage which is effected by peristaltic movements. In this
way are produced the spiral twists of the *chalazæ.* The ovum of the rabbit
receives in a similar manner an envelope of albumen as it passes along the
Fallopian tube.[1]

The liberation of the mature ovum from the seat of its
formation in the ovary occurs at certain periods, the periods of
rut or *heat,* which occur once or several times in the year; the
number of eggs which are liberated at one time varies from a
single one (in man) to many thousands. In general, sexual
intercourse is only fruitful when taking place during the period
of heat or rut.

The *semen* consists of a large number of corpuscles, which
are of a form peculiar to each species, and which are suspended
in a highly albuminous fluid, and which generally move through
it in a particular manner. The form of these seminal cor-
puscles (zoo-sperms, spermatozoa, or spermatozoids) is similar
in all vertebrata and in many invertebrata; they consist of a
globular, oval, or cylindrical (sometimes corkscrew-shaped) body
or head and a fine tolerably long thread or tail, which is con-
tinually engaged in a whip-like movement. In invertebrate
animals numerous other, in part motionless, forms are seen.

Impregnation consists in contact of the semen with the
liberated ovum. This contact happens either within the female

[1] According to recent researches (His) the yolk of the bird's egg consists, in
addition to ovum proper (principal yolk) and the germinal vesicle and the accessory
yolk, of cells of the membrana granulosa of the follicle which have wandered through
the zona. In the mammalian egg, at least, only a small part of the cells of the mem-
brana granulosa wander into the egg, the remainder forming the epithelium of
the follicle and the ' discus proligerus.'

organs of generation, into which the semen is conducted, or outside of them, by the semen being poured over the previously extruded ova, or by being accidentally brought in contact with the eggs, as by the surrounding water. Even artificial fertilisation is .possible. Very small quantities of semen appear sufficient to fertilise, provided that they contain spermatozoa (Spallanzani).

The union of the male and female bodies which is required in the first-mentioned mode of impregnation is denominated sexual intercourse or copulation. In the majority of animals it occurs during the period of rut, during which time, along with the special condition of the germ-preparing organs, in both sexes the desire for intercourse, ' sexual appetite,' awakens. Probably in all animals the act of copulation is accompanied by voluptuous sensations.

The nature of impregnation is as yet unknown. In all probability it is, above all, essential, in order that it should occur, *that one or more spermatozoa should penetrate the ovum.* At any rate spermatozoa have been found within the fecundated eggs of the most diverse species of animals. The entrance of the spermatozoa occurs, in eggs which possess a *micropyle,* probably through it, otherwise perhaps by an active penetration of the ovi-sac ; both processes have been observed to occur.

The development of the embryo commences soon after the contact or penetration of the semen, being brought about, or at any rate furthered by it, in an inexplicable manner. The spermatozoa which have penetrated disappear after a short time ; nothing definite is known in reference to the changes which they undergo.

Development of the Impregnated Egg.

The development of the egg begins in all cases with the formation of numerous cells, through a progressive division of the ovum ; this is known as *segmentation.* Out of the cells which are formed originate the organs of the embryo in so many ways that no general principles applicable to all animals can be laid down. In ova which possess a food-yolk (birds, amphibia, fishes, strictly even mammalia) only a partial segmentation occurs, *i.e.* the whole of the yolk does not take part in

the process, but only that part of it which contains the germinal vesicle, which is called the principal yolk or formative yolk. The non-segmenting food-yolk, which is derived from the granulosa cells of the follicle, undergoes no morphological changes, but it yields its chemical constituents to the embryo so as to build it up, hence its name.

The development of the ovum takes place in the majority of cases outside the maternal organism, in the most different localities suitable to the process. In the majority of cases a certain temperature is requisite for development, which is partly obtained by the choice of the locality in which the egg is deposited, partly afforded by the sun's heat, and, lastly, partly by the maternal body, given whilst it covers the eggs (hatching); this can also be artificially applied (artificial hatching).

The second condition necessary to development is the access of oxygen. In the developing egg, as in the already developed organism, processes of oxidation occur, which consume oxygen and yield carbonic acid. The exchanges of the gases with the atmosphere, or with the water which contains gases, takes place through porous openings. In many cases the development of the ovum takes place within the maternal organism in a dilatation of the efferent generative apparatus, *i.e.* in the uterus, as in mammalia and in man. The two conditions requisite for development are here realised in a very complete manner; the temperature is maintained by the sojourn in the equally heated maternal body; the respiration takes place by means of the very early developed vessels of the embryo, which form a capillary system in connection with a part of the uterine wall; the walls of the fœtal capillary system come into immediate contact with the maternal capillaries, which are also strongly developed at the above-mentioned part.

At this spot—in the 'placenta'—there occurs a passage of oxygen from the blood of the mother into that of the embryo, and of carbonic acid in the reverse direction. The same organ is the medium of the passage of nutritive matters from the body of the mother to that of the embryo. After development has proceeded to a certain point, the egg is expelled through the genital aperture, the process being denominated 'birth.'

Modifications of Development.

The development of the ovum into a complete organism similar to the one from which it is derived does not always take place continuously. In certain classes of animals development is arrested for considerable periods at certain stages; at these stages of development the organism manifests similar functions to those which are observed when it is completely developed, viz. voluntary motion, capacity to take food, to digest, &c. This is called the 'larval condition,' and the best known examples are afforded by the larval stage in the 'metamorphosis' of insects. Even reproduction occurs in such larval conditions, by fission and budding; when this occurs the process is termed 'alternate generation.' As larvæ generally possess a thoroughly different form, and as their life cannot be distinguished from that of the fully formed organism, numerous larvæ have been described as separate species before their origin and further development were discovered: This has specially occurred in cases of alternate generation; the larvæ which possess the functions of a fully developed animal, including the power of reproduction, and the forms of which differ in an extraordinary degree from that which they ultimately assume, have for long periods of time been held to be distinct animal forms, even to be animals belonging to different classes or orders.

The *leaf-louse* may be cited as offering the simplest example of alternate generation. From the fertilised ova of this creature, early in the spring, non-sexual young are developed, and these produce animals similar to themselves which are born alive; the latter, in their turn, give birth to a new viviparous generation, and the process is repeated during several generations, until finally, later in the autumn, young are born which are partly male and partly female; these copulate and produce fertilised ova which remain inactive during the winter; in spring the cycle of changes again commences. The viviparous generations cannot be looked upon as composed of parthenogenetic females, because they never change into the egg-producing females of the final generation (Leuckart).

A more complete example is furnished by intestinal worms belonging to the cestode class, *e.g.* by tape-worms (*tænia solium*).

The living tape-worm existing in the intestine of man consists of a head with suckers and hooklets, and of a chain of segments (joints), which are smallest near the head and then grow longer and broader. The smallest are the youngest, and these originate continually by a process of budding from the so-called neck. Every joint is to be looked upon as an individual, and

contains male and female organs of generation, which develop with age. Sexual congress takes place between these joints, so that the oldest always contain fertilised eggs already in a state of development. These joints (proglottides) are from time to time thrown off, and leave the body with the excrement. Presumably the ova, when they again directly reach a human intestine, can again develop into the heads of tape-worms and generate new joints; there would then be an alternation between two generations, one increasing by budding and one by a sexual process (hermaphroditic).

The usual process, however, consists in this, that the ova, previously referred to, find a host in one of the numerous animals into whose bodies they can be introduced with the food, and nearly always by preference the host, in the case of the *tænia solium*, is a particular animal species—the pig.

Here the hook-provided embryo bores its way to parts suited for its residence (the liver, the brain, the muscles, the tænia solium in the pig specially reaching the sub-cutaneous cellular tissue;—possibly a part of the way to the organs is travelled over by the embryo finding its way into the blood, giving rise to an embolism and being liberated again), and there develops a bladder-like appendage (cyst) into which it can occlude itself. Thus out of the tænia solium is formed the cystercus cellulosæ of the pig (measley pork), which, when the flesh is consumed by man, reaches his alimentary canal, where, by the action of the digestive fluids, it loses its bladder and acquires joints. In other cases, as in the echinococcus hominis (found in the liver, kidneys, &c., and derived from the tænia echinococcus of the dog's intestine), there originate within a headless bladder, ' acephalocyst,' which develops from the embryo, many small cysts with the heads of tæniæ, and within these there often occur new generations.

In this case two different kinds of non-sexual alternate with sexual reproduction, of which the one, which can pass through many generations, is by budding from the embryo bladder, the other by budding from the tænia-heads.

B. REPRODUCTION IN MAN.

The propagation of the human race is effected by a sexual process of reproduction, impregnation taking place internally, and the development of the embryo being intra-uterine. Birth occurs about 280 days after the impregnation of the ovum. Usually only one ovum, rarely two, still more seldom three or more ova develop at once.

The period of sexual maturity (puberty) generally commences in man between the ages of 13 and 17, being somewhat earlier in woman than in man, and somewhat earlier in hot than in cold climates. In addition to the development of the organs of generation and their appendices (as, *e.g.,* the hair which

covers the pudenda), and the display of the functions connected with this development (menstruation in woman, seminal emissions in man), there appear at this period many other corporeal changes, such as the development of the mammary glands and the growth of the *panniculus adiposus* in woman, the changes in the voice and the growth of the beard in man. At the same time there occur also certain psychical changes, and the sexual passion manifests itself.

The period of fecundity continues in woman until about 45 or 50 years of age; in man no certain limit has been ascertained to exist. In woman the close of the period of fecundity and the arrest of menstruation are associated with certain bodily changes, especially of the generative apparatus, which are ' comprehended ' in the term ' involution,' but in which the normal cannot yet be sufficiently distinguished from the morbid changes.

Formation of the Ovum.

The mature human ovum is globular, and has a diameter of $0.18-0.2^{mm}$. The external envelope is a tolerably thick, clear, structureless membrane, which presents the appearance of a clear ring (*zona pellucida*). No membrane has been discovered below this. The yolk is a tough granular protoplasm, probably contractile ; within it, situated usually excentrically, is the germinal vesicle, presenting the appearance of a clear bladder with a dark germinal spot. The existence of a food-yolk surrounding the principal yolk is probable. The chemical constituents of the human ovum are probably those mentioned at p. 533.

The formation of the egg takes place in the Graafian follicles of the ovary ; these are spherical bladders, which, when ripe, are about the size of a pea, and are embedded in the stroma of the ovary. Their wall is composed of a vascular capsule, composed of connective tissue, which is coated on its inner surface by a stratified epithelium (*'membrana granulosa'* seu *'germinativa'*). This epithelium is at a certain spot massed into a mound of cells (*cumulus* s. *discus proligerus*), in which the ovum lies embedded. The hollow space in the follicle is filled with a yellow albuminous fluid.

According to recent researches (Pflüger, His, Waldeyer, Koster, and

others) the development of ova and follicles probably takes place in mammalia and man in the following manner :—

The connective-tissue rudiment of the ovary, which is a part of the connective tissue of the Wolffian body, is covered by a layer of cylindrical cells distinct from the peritoneal epithelium; this very early growing thicker inserts itself into the simultaneously growing stroma of connective tissue. By this simultaneous growth there is formed in the ovarian stroma a cavernous system of tubes quite filled with cells (Valentin), the so-called egg-tubes ('Eischläuche ').

Some of these cells distinguish themselves soon by their size and appearance from the remainder; these are the ovum-cells (according to Pflüger primordial eggs, which by further division form ova). Later on, the tubes separate into divisions, of which each contains one, a few several egg-cells, surrounded by the smaller cells of the granulosa; in these divisions, *i.e.* in the rudiments of the follicles, between the cells, there is formed a cavity filled with liquid, which extends around and divides the cells into one set which lies in contact with the wall of the follicle (*membrana granulosa*), and into another which remains in relation with the other, but which surrounds the ovum (cumulus proligerus) which is now placed peripherically.

During their maturation the ova acquire their zona pellucida and food-yolk, both of which are presumably products of the layer of cells of the granulosa which lie immediately in contact with the egg (this layer is distinguished by the cylindrical form of the cells).

In cases where the food-yolk consists of cells, these are derived from the membrana granulosa, and have wandered through the zona. In the bird's egg all the cells of the membrana granulosa wander, and the yolk represents the entire follicle.

At determined intervals one or more of the follicles of the ovary reach maturity, *i.e.* their size and the distension of their walls increase so much, in consequence of the augmentation of their fluid contents, that they burst. As the follicles in ripening always approach the surface of the ovary, and as they lie before their rupture immediately beneath the capsule of connective tissue which invests the organ, the fluid contents, together with the ovum embedded in the cells of the *cumulus proligerus*, would be extruded immediately into the abdominal cavity. As, however, before the rupture of the follicle, the fimbriated extremity of the Fallopian tube is so apposed to the surface of the ovary that, cup-like, it embraces the follicle, the ovum enters the canal of the Fallopian tube, and is impelled through it into the uterus by the outwardly directed movements of the cilia of the epithelium which lines the tube.

The process of liberation of the ovum is associated with a capillary hæmorrhage from the uterine mucous membrane,

which constitutes the phenomenon of 'menstruation.' The liberation of ova occurs in woman during the whole period of her sexual life, except during pregnancy and lactation, at intervals of twenty-eight days, the hæmorrhage continuing for several days. Usually only one ovum is extruded at one time; rarely two or more are liberated.

In mammalia the liberation of ova (rut or heat) occurs more seldom, viz. once or several times in the year, but in them several ova are generally thrown off within a short period; in their case, too, a discharge of blood takes place from the organs of generation.

The object of the hæmorrhage appears to be to stimulate the uterine mucous membrane, so as to favour the reception of the ovum in the event of its being impregnated (Pflüger). In support of this view may be cited the fact that, in animals which possess several placental sites, at the time of 'heat,' blood merely exudes from those sites.

The broken and emptied Graafian follicle, which, at most, contains a drop of blood which has entered it during the process of rupture, undergoes special changes, some of which commence before the rupture. The cells of the membrana granulosa increase first, and become filled with a yellow fat, whilst the capsule becomes less and less distinguishable from the stroma of the ovary.

Thus originates the *corpus luteum*, which progressively recedes into the interior of the ovary. After it has attained a certain size (generally before the commencement of the succeeding menstruation, for one generally finds but one corpus luteum in the ovary) it shrivels into a cicatrix, which soon becomes imperceptible, and which sometimes contains crystals of hæmatoidin, which are derived from the extravasated blood. At the place where the ovarian capsule was broken there also remains a cicatrix, so that, as life advances, the originally smooth surface of the ovary becomes more and more puckered. During pregnancy the last formed *corpus luteum* is developed much more slowly, and reaches a much greater size, so that before the periodical liberation of ova was known such were alone spoken of as 'corpora lutea vera.'

The blood which is separated during menstruation is mixed with uterine mucus, with epithelium cells, and mucous corpus-

cles; it is probably to this admixture that the menstrual blood owes its decided alkalinity, and its inability to coagulate.

The processes which go on during menstruation are yet, in many respects, obscure; no sufficient explanation has yet been given of the cause of the periodic maturation of the follicles, nor of its relation to the external hæmorrhage, nor of the peculiar course which the follicles follow in the ovary before and after their rupture, but especially concerning the mode in which the apposition of the Fallopian tube to the ovary takes place. The discovery of specially arranged unstriped muscular fibres in the fold of peritoneum which supports the uterus, the Fallopian tubes, and the ovaries (Rouget) appears to offer an explanation for the majority of these phenomena. These muscular fibres must, in the first place, bring about the apposition of the orifices of the tubes to the ovary, and in the second place, by compressing the venous trunks, lead to a stasis of blood in the organs of generation; the consequence of this must be to cause a kind of erection in the vessels the structure of which is similar to that of the *corpora cavernosa*, leading to a hæmorrhage within the uterus, but in the ovary to an increase in the contents of a follicle due to the transudation, and ultimately to the bursting of the follicle.

The further changes which the liberated ova undergo will be discussed farther on, when the results brought about by impregnation are considered.

Formation of Semen.

Human semen in the condition in which it is evacuated is a very tough, white, alkaline fluid, possessed of peculiar odour, and assuming a more fluid consistence when exposed to air. It is a mixture of the secretions of the glands which empty themselves in the excretory passages, with the original secretion from the testicles; the latter is alkaline or neutral, is destitute of smell, and dries more readily.

The semen contains a large number of seminal corpuscles, about $0·05^{mm}$ long, the body of which is almond-shaped and terminates in a tapering tail. The movements of the spermatozoids are pendulum-like or wave-like vibrations of the tail, by which the body is driven forward in a straight line, at a rate varying between $0·05^{mm}$ and $0·15^{mm}$ in the second, until, meeting with an obstacle, its direction is altered. The movement of spermatozoa is most rapid in semen which has just been evacuated; it is slow or absent in semen from the testicle. The duration of the movement depends upon a variety of circum-

stances, which, in general, are the same as those which influence the ciliary motion.

The motion of spermatozoids continues longest in fluids the concentration of which is the same, or very nearly the same, as that of semen, and is especially active in the secretion of the seminal passages (as in the prostatic secretion, Cowper's secretion, &c.), as well as in that of the female genital organs. The motion very soon ceases in very dilute fluids, in water and in saliva. Quite independently of the state of concentration, the following substances arrest the secretion: many metallic salts, mineral acids, alcoholic and ethereal substances, &c. On the contrary, the caustic alkalies under certain circumstances restore the arrested movements of spermatozoa. The cause of these movements is quite unknown; some consider the head to be the active organ of movement (Grohe), and others the tail (Schweigger-Seidel, v. La Valette St. George); the relations between the movements of spermatozoa and those of protoplasm and of cilia have already been spoken of in Chapter VIII.

The principal chemical constituents of the semen are: albuminous bodies, protagon, fats, water, and salts (potassium salts, phosphates).

The formation of semen takes place in the testicle, the cells of the 'seminal tubes' furnishing the spermatozoa. The statements relating to the formation of the latter in man are not yet certain. Most probably several or many spermatozoa originate in one cell, from nucleated oval vesicles, of which each one develops at one end the tail of a spermatozoon; ultimately the parent cell falls to pieces, setting free the spermatozoa; occasionally fragments of the cell remain connected with the spermatozoa and admit of being recognised (Kölliker). According to other observers the semen-forming cells possess but one nucleus, and the nucleus grows as the head of the spermatozoid out of one side of the cell, whilst opposite to it the protoplasm of the cell grows out as the tail of the spermatozoid (v. La Valette St. George). The semen-forming cells originate by division from the glandular cells, which lie in the axis of the tubuli seminiferi (lately different statements have been made on this matter, which are, however, doubtful). The fluid part of the semen originates by unknown secretory processes in the tubuli seminiferi; in all probability the specific constituents of the fluid proceed from the same cells which furnish the spermatozoa. The spermatozoa of the tubuli seminiferi exhibit either no movements or only slight ones. The formation of semen appears to proceed continuously. Nothing is known in reference to the nerves which preside over this secretion.

The semen, when formed, after it has passed through the

spongy cavities of the ' corpus Highmori' and the canals of the *epididymis,* is carried by the *vas deferens* into the *vesiculæ seminales,* where it accumulates. On its way it mixes with the secretion of the mucous membrane of the vas deferens, the inferior extremity of which presents racemose glands, as well as with the secretion of the vesiculæ seminales.

The emission of semen takes place by reflex action through irritation of the penis, during sexual intercourse, during sleep under the influence of weak irritations associated with voluptuous dreams (seminal emissions caused by pressure of urine).

Under normal circumstances, erection of the penis must precede emission of semen, *i.e.* the three corpora cavernosa become filled with blood, so that the penis becomes lengthened and stiffened, and assumes a rounded prismatic form ; at the same time it becomes erect, and slightly concave on its dorsal surface. The nature of erection has not yet been sufficiently made out.

The corpora cavernosa constitute a communicating system of cavities, in which open the finest twigs of the arteries which run in the septa, and from which the veins proceed. As the septa contain smooth muscular fibres, and can therefore actively alter the lumen of the corpora cavernosa, two explanations of erection are possible, viz. : 1. The flow of blood out of the corpora cavernosa may be hindered by compression of the efferent veins. 2. An increased flow of blood into the corpora cavernosa may occur by the cessation of a tonic contraction which is present during rest (Kölliker).

Both phenomena appear actually to occur, as the following experiments prove : 1. Diminution of a tonic contraction of blood-vessels ; in the dog irritation of the *nervi erigentes* (fibres which proceed from the sciatic to the hypogastric plexus) causes erection (Eckhard). During this irritation any arteries of the penis which may have been cut across bleed more freely (Lovén); erection can therefore not merely be due to a hindered efflux of blood, but it must depend upon the abolition of a contraction of vessels, the mechanism of which is not known ; the pressure of blood in the vessels of the penis, even during the strongest erection, only amounts to one-sixth of the pressure in the carotid artery (Lovén). The action of the nerves which influence erection may be placed side by side with

that which the fibres of the chorda tympani exert on the salivary glands.

The vaso-motor nerves of the penis are contained in the *pudendal nerve* and in the *nervi dorsales penis;* a section of these alone does not cause erection; it however prevents erection in the future (Hausmann and Günther).

2. A compression of the efferent veins appears to occur, especially when erection is at its height ; this is effected (*a*) by the m. transversus perinæi, through which the venæ profundæ pass (Henle); (*b*) by trabecular projections, composed of smooth muscular fibres, into the veins which compose the plexus Santorini (Langer); (*c*) by the venæ profundæ themselves passing through the corpora cavernosa (Langer). The immediate centre which presides over erection appears to exist in the lumbar portion of the spinal cord (Goltz). After cutting across the cord between the cervical and dorsal regions, mechanical irritation of the penis of dogs still leads to reflex erection (strong irritation of sensory nerves prevents this, as it does other reflex actions), though not after destruction of the lumbar portion of the cord. The brain is in connection with this centre, as results from the fact that erection of the penis is brought about by psychical conditions, further that it follows irritation of the crura cerebri, of the cervical portion of the cord (Ségalas, Budge, Eckhard). Erection often occurs in persons who die by hanging.

The arteries which lead to the corpora cavernosa ('helicine arteries') follow a very curved course, so that a great increase in the volume of the penis may occur without any dragging of the arteries.

Sexual Intercourse.

Whenever the sexual passion is excited, erection sets in, and it precedes the emission of semen. The latter phenomenon only occurs after mechanical irritation of the penis, as occurs during sexual intercourse by its friction against the rugose walls of the vagina. It therefore occurs as a reflex movement.

The emission of semen from the vesiculæ seminales into the urethra probably occurs by peristaltic contraction of the vas deferens and vesiculæ seminales, whilst the emission from the urethra is the result of rhythmical contractions of the bulbo-

and ischio-cavernous muscles. The passage to the bladder is
shut off by the erection of the ' caput gallinaginis,' which at the
same time prevents the passage of urine during erection. The
secretions from the prostate and from Cowper's glands mingle
with the semen which is excreted. Even in the genital organs
of woman, as a result of the sensory irritation which takes place
during coitus, certain reflex movements occur, which probably
further the passage of semen into the most internal organs.
Amongst such movements have been surmised the assumption
of a more perpendicular position by the uterus, which is perhaps
due to an erection of this organ (Rouget), and, probably, peri-
staltic movements of the uterus and Fallopian tubes, taking
place in the direction of the ovaries (such movements have at
any rate been observed to occur in the lower animals). Such
movements would explain how a portion of the semen is con-
ducted to the ovary, in spite of the movements of the ciliated
epithelium, which are opposed to its passage, as the irregular
movements of the spermatozoa could not be utilised in effecting
the passage upwards. After emission of semen erection very
soon ceases, as well as the psychical and physical excitement
which accompanies it ; the latter disappears more rapidly in
man than in woman. In both sexes there ensues an exhaus-
tion, which continues for some time.

Impregnation.

The seat of contact between ovum and semen has not yet
been determined with certainty, but in all probability it occurs
generally in the ovary itself, or in the vicinity of the Fallopian
tubes, seeing that in mammalia, after intercourse has taken
place, the surface of the ovaries is generally covered with sper-
matozoids (Bischoff) ; in this way is to be explained the occa-
sional occurrence of ovarian and abdominal pregnancies. Closely
connected with this question is the one as to whether, with
sexual intercourse, there is associated a liberation of ova similar
to that which occurs during menstruation, or whether, in fertile
coitus, only the ova which are liberated before or after menstru-
ation are impregnated. In favour of the latter view is the ana-
logy with mammalian animals which can only be impregnated
during the ' period of heat.' As the human female can be

impregnated at any time, we must, if intercourse cannot effect a liberation of ova, suppose that either the still present ovum of the last menstruation remains capable of fertilisation, and is actually impregnated, or that the semen remains in the female generative organs, perhaps even in contact with the ovary, until the next ovum is liberated, and is still able to fertilise it. Probably both processes occur. Concerning the process of impregnation and the first stages of development, there exist, in the case of man, no direct observations. We are therefore here compelled to reason by analogy from the other mammalia, as must necessarily be done in the exposition which is to follow of the processes of development. The youngest fecundated ova obtained as a result of miscarriage, or of the death of the mother, exhibit only tolerably advanced stages of development.

The impregnated egg is most probably impelled by the ciliary motion of the mucous membrane of the Fallopian tube into the uterus, to the mucous membrane of which it attaches itself, and in which it is usually found embedded. Presumably the process proceeds in such a manner that the surrounding parts of the mucous membrane increase in size, and grow over the ovum, the portion which has grown over, which is called the ' decidua reflexa,' increasing in size with the ovum.

According to another view the ovum places itself behind the uterine mucous membrane (decidua vera), and thrusts it before itself; according to Funke, the process consists in the ovum sinking into a uterine gland, as is really the case in the guinea-pig, and perforating its base.

At a later stage of development, after the embryonal vessels have been formed, an intimate interlacement with those of the mother takes place (placenta). The excessive development of a corpus luteum (verum) during pregnancy points to the periodic liberation of ova being interrupted by it. The interruption usually continues during lactation, as is evidenced by the fact that menstruation usually is absent, and especially because fresh corpora lutea are usually not formed in suckling women.

An incipient formation of a decidua appears to occur with each liberation of an ovum, the uterine mucous membrane being swollen; and this appears to be the cause of the menstrual hæmorrhage (Pflüger).

C. DEVELOPMENT OF THE OVUM IN THE MAMMALIA AND MAN.

Segmentation.

The first process in the development of the ovum is that of *segmentation.*

It begins in mammalia as early as a few hours after the contact of the semen with the ovum, or after the entrance of the spermatozoids into the yolk (perhaps even earlier), so that the ovum only reaches the uterus at a tolerably late stage of development. Segmentation consists in a progressive cell-division, by which each spherical cell splits up into two half-spheres. Whether the first cell is identical with the 'germ-cell' (with the principal yolk), or whether it first originates by transformations of that cell is doubtful, and the same remark applies to the germinal vesicle, which is invisible before segmentation, as well as to the manner of cell-division and the division of the nucleus.

Segmentation proceeds very rapidly (its duration in man is unknown; in the rabbit it lasts some days, and in the dog more than eight days) and furnishes in the end a large number of small, spherical, strongly refracting cells, which together present a mulberry-like appearance.

During segmentation the ovum, whilst in the Fallopian tube, loses the *discus proligerus,* and either surrounds itself, as the rabbit's ovum, with accessory envelopes, or the zona pellucida first receives in the uterus (as in the human subject) the first envelope of fine radially arranged villi, which ramify and form a thick villous covering around the ovum; the zona then receives the name of *chorion* (frondosum).

Rudiment of the Embryo.

The disposal of the cells which have been produced in the process of segmentation for the purpose of building up the embryo commences with the deposition of their greater part on the inside of the zona pellucida, to form a closed membrane which is called the germ-vesicle (' *Umhüllungshaut,*' Reichert). At a certain part of the membrane a more considerable accumulation of cells takes place, destined directly for the formation

of the embryo, and this is called 'the germinal area.' The cavity which results from the deposition of cells, as well as from the enlargement of the ovum, is filled with fluid, or in eggs which possess a food-yolk, contains the latter.

In order to understand the development of the embryo a somewhat different consideration of the fully developed animal body than that usually given by descriptive anatomists is requisite.   Let us conceive a mammal with a short straight alimentary canal, and let us lose sight of all glandular organs; the body may then be considered as a tube, the lumen of which is the lumen of the alimentary canal and the wall of which is composed of many concentric layers, viz. (from within outwards): intestinal mucous membrane, muscular coat of intestine, serous coat of intestine, parietal layer of peritoneum, muscular layer of trunk, osseous layer of trunk, skin covering trunk.   All these layers grow together; only between the visceral and parietal layers of the peritoneum, up to the mesentery situated in the middle line behind, there is no fusion, but a cavity, the pleuro-peritoneal cavity, which is, however, empty, so that its walls are always completely in contact with one another.   The ideal tube which we are imagining possesses complete symmetry.   Its extremities, which have no openings, may be looked upon as bulky outgrowths from the external wall of the tube.

The embryonic development of the tube takes place in general in the following manner: the wall arises in the commencement as a flat thickening of the first-formed *germ vesicle* which everywhere surrounds the ovum; this thickened spot splits up by degrees into the different layers which correspond to the strata in the wall of the ideal tube.

The cavity, however (the intestinal cavity), is a part of the germ-vesicle, which separates from the rest by the thickened portion of the vesicle—that which is to form the wall of the embryo—partly shutting itself off from the rest of the vesicle, in the form of a lengthened tube.   The main portion of the germ-vesicle (which is not included within the embryo) is then called the *umbilical vesicle,* and the canal-shaped communication which by the ever increasing constriction becomes progressively narrower, and establishes a communication between the cavity in the embryo (intestinal cavity) and that of the umbilical vesicle, is called *the umbilical duct* or 'ductus vitello-

intestinalis seu omphalo-entericus.' The ultimately ring-shaped place of constriction is *the navel;* as the thickening and even the division into layers of the germ-vesicle does not limit itself to the portion which becomes constricted, but extends beyond the point of constriction towards the peripheral parts of the vesicle, it follows that even the wall of the navel consists of several embryonic layers.

The formation of layers over the germinal area of the germ-vesicle, which, in great part, begins even before the commencement of the shutting off of the embryonic cavity, is variously described. Only one view, which in the main is Remak's, will here be given; the others will be, however, cursorily examined.

Three layers—the three layers of the blastoderm—form in the smooth at first oval, then hour-glass-shaped thickening of the germ-vesicle. The most external or uppermost—' the *epiblast*,' the sensory layer, is the seat of the cutaneous epithelium with its appendages, the glands of the skin, and of the central organs of the nervous system (brain and spinal cord) with its appendages, the organs of the senses.

The central nervous system originates in the central (axial) part of this layer in the so-called *medullary folds;* the epithelium of the skin is formed from the peripheral part or ' *corneal layer* ' of the epiblast.

The innermost of the three layers of the blastoderm—' the *hypoblast* '—is the seat of the intestinal epithelium with its appendages, viz. the epithelium and the glandular cells of the glands which open into the intestine. Between the epiblast and the hypoblast lies the *mesoblast*, the motor and germinative layer from which all the rest—all the parts of the body which consist of connective tissue, muscles, vessels, and nerves, as well as the urinary and generative organs—are formed. This layer splits up very early into two plates; the external forms the wall of the trunk, the internal forms the wall of the intestine, with the exception of the epithelium; the space between these secondary layers constitutes the already mentioned ' *pleuro-peritoneal cavity*.' Inasmuch as the division into these two layers is arrested in the middle line, there is here established a fusion between the wall of the trunk and of the intestine, and this is the seat of the mesentery. (Compare below, Fig. 42, II., III., IV.)

Processes of Development in the Germinal Area.

In each of the three layers of the blastoderm there follow, in addition to the already mentioned process of constriction, certain processes of development by which they undergo transformation.

The chief of these processes are: 1. In the *epiblast* the *laminæ dorsales* or *medullary folds* separate from the corneal layer and form a tube. 2. In the *mesoblast* the first commencement of a skeleton takes place; further, the division already alluded to and the formation of a vascular system commences. 3. From the *epiblast* and *hypoblast* processes of epithelium grow into the tissues from out of the middle layer, so that there are formed hollow processes which are in part enclosed in the body cavity, and form glands.

Epiblast.

1. The first process to be mentioned is the one which first occurs. In the centre of the medullary fold a longitudinal groove is formed, dividing it into two symmetrical halves, which curve towards one another, drawing over themselves the corneal plates which are attached to them. The cause of this is the growing forwards of the processes of the middle layer, which tend to press themselves between the medullary plates, which are curved towards one another, and the corneal plate. Ultimately the medullary folds are closed, so as to form the medullary tube, and the corneal plates still attached to the point of union are, finally, completely separated from it by the union of the two lateral appendages of the middle layer, in such a manner that the medullary tube is thenceforward entirely enveloped in a prolongation of that layer. This envelope forms the spinal arch, together with the muscles, the ligaments, and the skin of the back (which last receives a covering from the corneal layer, viz. the epidermis), and at the anterior extremity (head) the cranial capsule.

The medullary tube becomes the spinal cord and brain; its interior is converted into the central canal of the cord, with its connection in the brain—the so-called ventricles of the brain. Compare below, Fig. 42, II., III., IV.)

Mesoblast.

2. The simultaneous phenomena of development which take place in the *mesoblast* concern the vertebral system.

The centre of this system is a streak which is very early developed, and which runs in the median plane of the embryo, and which is called the 'chorda dorsalis.' On each side of this there appear two longitudinal plates, *the protovertebral plates*, which by transverse lines subdivide themselves into a number of *protovertebræ*. The remainder of the mesoblast, so far as it belongs to the germinal area, forms 'the lateral plates.' The *protovertebræ* undergo the following changes: they develop 'spinal processes,' the influence of which upon the formation of the canal of the cerebro-spinal organs and upon the union between this and the separated corneal plates has already been mentioned. Internally the protovertebræ grow around the chorda dorsalis. (See below, Fig. 42, II., and following.)

Their substance is converted into various tissues, viz. into the vertebral column with its appendages, into the ribs and the muscles pertaining to them, into the spinal nerves and the skin of the back. The bodies of the vertebræ originate in the part which surrounds the notochord, in such a manner that in the middle section of each protovertebra there is formed an intervertebral cartilage, and from the fusion of adjacent halves of the protovertebræ a persistent vertebral body originates.

In the lateral plates there occurs further the already mentioned splitting up of the embryonal wall into the two layers; the internal attaches itself to the hypoblast, and forms with it the *splanchnopleure*, the external attaches itself to the epiblast, and forms with it the *somatopleure*. The separation between these two layers forms the *pleuro-peritoneal cavity*; the internal undivided edges of the *lateral plates*, advancing together little by little on the ventral side of the vertebral column, form the so-called *middle plates*, which are the foundation of the *mesentery*, and fœtal urinary and generative organs. The former of these two sets of organs originate as a string-like thickening of the middle plates, which later on becomes hollow; according to some as an invagination of the pleuro

peritoneal cavity—the *Wolffian canal.* For the further development of this organ, and the other urino-generative organs, see below.

The third process which takes place in the mesoblast is the development of the *vascular system.*

This system first originates in that layer of the mesoblast which goes to form the *splanchnopleure,* and makes its way outwards in the yet undivided peripheral part of the mesoblast. The manner in which the vessels and the blood are formed has not been accurately determined, yet, according to the majority of statements, it occurs as follows : cellular trabeculæ are interwoven so as to form a network ; the peripheral layers of cells are then converted into vascular parietes, and the contained cells become at first colourless nucleated blood-corpuscles. According to a new view (Klein) the vessels originate in cells which become hollow, which lengthen out and run together, and from the nuclei of which the blood-corpuscles are formed.

The area over which blood-vessels are formed is considerable, occupying an important circularly-bordered portion of the germ-vesicle, which is called the *area vasculosa.*

Of all vessels the first formed is *the Heart ;* it originates in the most anterior part of the splanchno-pleure which has already become closed into a tube.

The following may serve to explain the position of the heart: the amnion-fold is formed more rapidly at the head and tail than at the sides. At a certain stage of development the *embryonal wall* which is shutting itself off from the *germ vesicle* resembles a shoe somewhat *trodden down at heel* (see Fig. 42, I.), the free borders of which pass into the main part of the germ-vesicle. The opening of the shoe represents the still widely open *navel;* the shoe cavity represents the interior of the intestine. Along the middle line of the sole of the shoe (which represents the dorsal surface of the embryo) the cerebro-spinal tube would be situated. The wall of the shoe is throughout double, up to a streak in the middle line of the sole (the mesentery) ; at the end of the shoe and on the uppermost part of the anterior layer (the shoe being supposed to be suspended vertically with the heel downwards, but with the opening towards the observer) the wall is also single, the body—and intestinal—wall being united. This unsplit upper part of the anterior wall is called the *' pharyngeal plate.'* From the cavity of the germ-vesicle one may pass through the navel, into the anterior part of the cavity of the embryo, which has now already assumed the shape of a tube (this part, which is transformed into the *foregut,* is called the *' fovea cardiaca '*), as well as into the posterior, shallower, *' foveola posterior.'* That part of the wall of the *' fovea cardiaca '* which is directed towards the

germ-vesicle (the anterior wall of the hypothetical shoe) is, below the '*pharyngeal plate*,' also double like the main part of the sole. Of the two layers the inner one represents the anterior wall of the foregut, and the external that portion of the pleuro-peritoneal cavity which ties in front of the intestine. (Refer to Fig. 42, I., V., VIII.)

The heart originates in the median line anteriorly, according to some (Remak), as a cylindrical thickening of the anterior wall of the foregut (see Fig. 42, V., VI.), which thickening soon becomes hollowed out, and appears to be in connection with the remaining vessels; according to others (Schenk, Oellacher), as a process of the wall of the foregut, which shuts itself off and grows forwards into the cavity lying in front of the intestine, referred to in the preceding paragraph. The vessels which are connected with the heart are to be followed in two directions. The arterial vessels commence with two aortic arches starting from the anterior extremity of the heart, which curve inwards and backwards along the pharyngeal plate and which, separated at first throughout the length of the chorda dorsalis, later on unite to form the aorta, and terminate in the arteriæ iliacæ communes.

Instead of one there are generally several (three) aortic trunks on each side, which, however, again unite on each side to form an aorta or aortic root. On each side there springs .from the aortæ a series of vertically ascending arteries, which run on the sides of the splanchnopleure, and which go to the *area vasculosa*, where they ramify; these are called the *omphalo-meseraic* arteries. Two venous trunks pass into the posterior end of the heart through a short common trunk; these vessels also are distributed over the *area vasculosa* and are called the *omphalo-meseraic veins*.

Both the above sets of vessels communicate through a circular vessel which limits the area vasculosa and which is termed the *sinus terminalis* (see Fig. 42, I.) This system of vessels probably serves as a first respiratory apparatus, as well as to convey to the fœtus the nourishment which is yielded by the contents of the germ-vesicle. It disappears early in proportion as the contents of the vesicle are of little importance in nutrition, and is at a later stage replaced by the allantois, which subserves the same functions. As soon as it is formed, the heart begins to pulsate, so that the blood corpuscles com-

mence at once a somewhat irregular circulation through the newly-formed vessels.

Hypoblast.

From the inner layer, the development of which commences latest, processes are protruded which grow into that part of the mesoblast which is contained in the splanchnopleure,[1] and form the small glands of the alimentary canal, as well as the liver, the pancreas, and, in addition, the lungs and the permanent kidneys. It is easy to see how the protrusion of the hypoblast must form the epithelium, or the cells of a glandular canal, whilst the invaginated splanchnopleure must form the connective tissue, the blood-vessels, the nervous and the muscular surroundings (the basis of the gland). If the protrusion proceeds so far that even the splanchnopleure is protruded, as in all large glands, the protruded intestinal wall must evidently project into the pleuroperitoneal cavity, as is the case in reality with all the glands which open into the intestine and which are surrounded by peritoneum.

The liver originates by the protrusion of two hollow processes (primitive hepatic ducts) from the foregut, close to the navel; the finest branches form the very complex network of hepatic canals, which, with the blood-vessels, constitute the parenchyma of the hepatic lobules. The larger canals are the biliary ducts, and a projection from one of the primordial canals forms the gall-bladder. The liver grows around the trunk of the omphalo-meseraic vein, which communicates with its vessels. One of the intestinal veins which enter into it, and which is permanent, forms later on with those branches *the portal vein.*

Opposite to the liver, and starting from the posterior intestinal wall, there arises by ramifications, and afterwards hollowing out, an outgrowth which is at first solid, the *pancreas.*

A further double projection from the anterior wall of the intestine, but above the heart, and which penetrates the pleuro-peritoneal cavity, forms *the lungs*, with their *bronchial system*, the entrance to the lungs being therefore situated in the foregut (later the pharynx). For the development of the kidneys see p. 561. Lastly, the thyroid and thymus glands have to be con sidered; the first arises as a vesicular outgrowth from the anterior wall of the foregut, which shuts itself off, then by further processes of development

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[1] By this it is not intended to ascribe in any way an active part to the epithelium; it is indeed more probable that the in-growth of epithelium is conditioned by the growth of the splanchnopleure.

divides into two symmetrical cavities, which respectively give rise to secondary cavities. The thymus gland is formed in a similar manner. The spleen, lymphatic gland and follicles, and the suprarenal capsules, originate from the mesoblast.

Peripheral Processes of Development.

Side by side with all the processes of development which have been described as proceeding in the germinal area there are other processes taking place in the peripheral part of the germ-vesicle, which have for their object to permit the embryo to develop freely on all sides, by embedding it in a fluid (amnion), and also to bring the fœtal blood into relations permitting of diffusion-changes taking place between it and the maternal blood, whereby nutrition and respiration are rendered possible ('*allantois*').

1. Development of the Amnion.

It has already been mentioned that a cleavage of the germinal area into blastodermic layers proceeds beyond the embryonal area to the peripheral parts of the germ-vesicle, and that the same is true of the cleavage of the mesoblast. The latter cleavage, however, does not extend over the whole germ-vesicle, but only so far as the area vasculosa extends. Here the superficial layer ceases, so that at this spot, provided that the epiblast has been broken through, the space between the two layers of the mesoblast, and ultimately the pleuro-peritoneal cavity, may be reached. The peripheral parts of the external portion of the mesoblast ('Hautplatte') now rise up from the germ-vesicle, and arch backwards on all sides of the embryo, driving the epiblast before them, and coming from all sides join above the embryo, enclosing it in a sac which is called the amnion; the layer of the epiblast which is enclosed lines the inner surface of the amniotic sac.

The amnion is filled with a serous fluid, by which the embryo is surrounded on all sides; besides the normal constituents of transudations, it contains secretions from the skin and nitrogenous products of oxidation, presumably as a result of diffusion from the allantois.

2. Formation of the Allantois.

Near to the caudal end of the embryo in the region of the navel there originate two solid accumulations of cells, which grow from the external layer of the mesoblast, and which soon unite. Into this out-growth, which lies close to the splanchnopleure, there grows a process of the posterior part of the intestine in such a manner that a vesicular cavity is formed ; this bladder, *the allantois*, grows out of the embryo between the somatopleure and the splanchnopleure, reaching the space between the amnion and the germ-vesicle ; growing always more and more extensive, it envelops the amnion, and reaches the inner wall of the *chorion*, with which it becomes connected over a greater or smaller surface. The communication between the posterior part of the intestine and the allantois forms the *cloaca*, into which empty themselves the fœtal urinary organs. The part of the allantois which becomes small, and which passes through the umbilical orifice, is called *the urachus*. The allantois is highly vascular. The arteries, the *umbilical* arteries spring from the common iliacs ; they lead to a well-developed capillary system, the loops of which enter the chorionic villi ; the veins unite to form the single *umbilical vein*, which, returning to the embryo, opens into the omphalo-meseraic vein, and thus communicates (as the *portal* vein) with the blood-vessels of the liver ; it sends a branch directly to the *vena cava inferior (ductus venosus)*.

The well-developed *villi of the chorion*, which contain the blood-vessels of the allantois, grow into the interior of the uterine mucous membrane, in which, at the corresponding spot, corresponding capillary loops are formed. The two sets of vessels together form the placenta, in which an exchange by diffusion proceeds between fœtal and maternal blood, for the purposes of respiration and nutrition ; the blood of the umbilical vein is therefore necessarily brighter (more arterial) than that of the corresponding arteries, exactly as at a later period of existence the blood of the pulmonary arteries and veins differ. The umbilical vesicle and the area vasculosa now lose their importance, and, together with their blood-vessels and the umbilical duct, shrivel together so as to form a thin string. The

fluid which the allantois contains is a transudation containing the secretion of the primordial kidneys, with some nitrogenous products of oxidation.

Whilst in man only one placenta is developed, animals possess several placental sites, so that the villi of the *chorion* enter the villi of the decidua in many places.

Final Stages of Development of the Embryo.

If we imagine the body cavity of the embryo to have been shut off from the germ-vesicle, the umbilicus will consist of two concentric tubes; the inner (the omphalo-meseraic duct) connects the intestine with the umbilical vesicle; the outer is formed by skin, and connects the abdominal wall of the embryo with the amnion. Between these concentric tubes there exists a circular space, through which the pleuro-peritoneal cavity may be reached, and through which the urachus comes.

By a simple process of separation by constriction, an intestinal tube, closed on all sides, is formed, which is united in the median line posteriorly to the body cavity (by the mesentery), and to the whole upper end of the body. Subsequently there are formed an anterior and a posterior intestinal opening. In the anterior part of the centre of the pharyngeal plate, close below the fore-brain, there is formed a depression into which the epiblast passes. This depression becomes deeper and deeper, and ultimately opens by a fissure into the upper end of the fore-gut (pharynx), forming the buccal and nasal cavities.

Further, there are formed on the lateral parts of the pharyngeal plate three gutter-shaped cavities of the hypoblast, which run from before backwards; these ultimately break through the pharyngeal plate, and form on each side three *visceral* or *branchial clefts*, and later on yet a fourth, by the hypoblast making a border, as the mucous membrane gives an external mucous edge to the lips; between each pair of pharyngeal plates there remains a *pharyngeal* or *branchial arch*, which is so arranged that on its inner side an aortic arch runs from before backwards. Along the pharyngeal arches thickenings arise from before backwards, and ultimately meet. The space between the skull and the first pharyngeal arch is taken up by the buccal and nasal cavities; the first pair of branchial arches is converted into a lower jaw and the neighbouring parts of the

cranium; as, however, it sends two branches into the common buccal and nasal cavity, which grow so as to meet, and which develop into the upper jaw and gums, a separation between the buccal and nasal cavities is ultimately effected. (It is from an arrest in the development of these processes that hare lip and cleft palate result.)

The remaining visceral clefts unite, the branchial arches furnishing the hyoid bone, a portion of the laryngeal cartilages, the skin of the neck, &c., by processes which cannot here be examined in detail. The tongue originates as an outgrowth from the inner side of the lower jaw. The posterior intestinal opening originates in a perforation of the *cloaca*, which is the common termination of the intestine and the allantois.

This common aperture is afterwards subdivided by a bridge, the *perinœum* (which is an outgrowth of the wall which separates the intestine from the allantois), into one connected with the bowel, viz. the *anus*, and into one communicating with the allantois (opening of the *uro-genital sinus*).

The first pair of visceral clefts unite, except where an opening is left, which is the rudiment of the external auditory meatus. The second, third, and fourth clefts unite completely; as the aortic arches bend back from the inner side of the branchial arches, and take with them the mesoblast, the third and fourth clefts grow deeper.

Of the remaining processes of development the following must be mentioned :

1. The 'medullary or neural tube,' the cavity of which continually diminishes by an increase of the thickness of its walls, very early shows, at its dilated cerebral end, two transverse depressions which mark off three *cerebral vesicles*. Each vesicle carries on either side a vesicular outgrowth, which subsequently becomes pedunculated, which represents the rudiments of the three higher organs of special sense with their respective nerves —the first is the olfactory, the second the optic, and the third the auditory; the vesicles are the rudiments of the peripheral nerve distribution. In the optic vesicle, which is immediately beneath the corneal layer, a vesicular involution of the latter takes place, which ultimately becomes shut off and forms *the lens* with its *capsule*. The optic vesicle thus invaginated in itself becomes converted into an hemispherical body, by the

anterior half (the *retina*) being placed in close apposition with the posterior (the *choroid*). Between the lens and the retina there then originates the *vitreous body*, and around, by a process from the mesoblast, the *sclerotic*, which unites with the portion of the skin which covers the eye so as to form the cornea.

The three cerebral vesicles represent, from before backwards, the *third ventricle*, the *aqueductus Silvii*, and the *fourth ventricle*. The first gives off a new vesicle on each side, the interior of which represents the *lateral ventricles* (the communication between these and the primitive vesicle is formed by the *foramen of Munro*), and their walls represent the cerebral hemispheres; the lateral vesicles in man outgrow all the others.

In a similar manner the third cerebral vesicle sends out two *cerebellar* vesicles. Between the first and the second vesicle there arises early a tolerably sharp constriction, so that the former bends around the anterior extremity of the embryo.

The cerebral ganglia (optic thalami, &c.) arise as a thickening of the vesicular walls.

Statements vary as to the origin of peripheral nerves and ganglion-cells. The majority of authorities believe them to originate in the mesoblast; others (Hensen) believe the axis cylinders to arise as outgrowths from the ganglionic cells of the central nervous system into the mesoblast, which furnishes, however, the sheath and white substance of Schwann.

2. The intestinal canal forms at first a simple tube, which is only slightly bent in the centre, where the mesentery is longest.

In the vicinity of the liver a dilatation of this tube occurs, marking the position of *the stomach*, which subsequently, by a movement of rotation, takes up its persistent transverse position and thus presents a *fundus* and two *curvatures*. By an elongation of the intestinal tube, and a simultaneous elongation of the mesentery are formed the coils of the small intestine and the curves of the large intestine. That piece of the omphalomesenteric duct which lies within the embryo breaks at the navel and forms a rudimentary appendage of the lower part of the ilium.

3. The heart, which in the beginning is a straight tube situated in the middle line, very early alters its form, so that its

venous (posterior and inferior) end bends itself towards its arterial end, so that the whole organ, with the origin of the veins, takes the form of an S (see below, Fig. 42, I.). The cause of this is that during a certain time the aortic arches increase in number posteriorly, whilst those situated anteriorly disappear; hence the anterior part of the heart is thrust backwards, whilst the venous end retains its original position. Three parts of the heart, which contract one after the other, may now be recognised, viz. *sinus venosus* (from which the two auricles afterwards spring), *ventricle,* and *bulbus aortæ.* A longitudinal partition wall is now formed, at first in the ventricle and afterwards in the auricle (being incomplete here), whereby two separate ventricles are formed, and two auricles communicating through the *foramen ovale.* Of the three remaining pairs of aortic roots, the first forms the carotid and subclavian (on the right side the common trunk persists); the second forms on the left side the permanent aortic arch, which leads to the primitive descending aorta, and from which the vessels of the first pair spring; the right branch disappears.

The third pair furnishes the pulmonary arteries; the right arch disappears, except its pulmonary branch, and the left remains connected with the descending aorta, the connecting piece forming the *ductus arteriosus* (duct of Botal). Ultimately the bulbus arteriosus divides itself in such a manner that the section which gives off the pulmonary arteries remains connected with the right ventricle, whilst the remainder, with the arch of the aorta, remains attached to the left ventricle. Even then all the blood can pass from the right heart into the aorta, partly through the foramen ovale, and partly through the ductus arteriosus. It is only after birth, when respiration through the lungs has commenced, that both these communications are closed, and thenceforward the whole of the blood of the right heart is carried to the lungs.

4. *The internal urinary organs* are developed in the following manner: the structure in which they originate, the *Wolffian duct,* is at its upper end closed, and communicates below with the posterior part of the intestine (*foveola posterior*). The anterior end of the duct sends inwards a row of little blind canals, which are in part furnished with *glomeruli* (derived from the mesoblast). Thus arises the *Wolffian body,* of which one

part, the primordial kidney, discharges the functions of a kidney, whilst the remainder (the sexual part) goes to form the organs of generation.

The *permanent kidneys* are formed (Kupffer) by a tubular protrusion from the tail-end of the Wolffian duct; this protrusion pursues a course parallel to that of the primordial kidneys, and grows upwards as the rudiment of the *ureters*; the upper end grows into a mass of cells derived from the mesoblast (parenchyma of the kidney), and thus originate the *pelvis of the kidney* and the *calyces*. The *tubuli uriniferi* are either (Remak) further outgrowths from the calyces, the dilated ends of which (*capsules*) surround the glomeruli, or (Kupffer) they originate independently in the kidneys (from the periphery outwards), and only afterwards open into the calyces. (For the development of the urinary bladder, the reader must refer to the paragraph relating to the external organs of generation.)

5. The *internal organs of generation* are originally hermaphroditically disposed in both sexes. The peritoneal squamous epithelium which invests the free surface of the Wolffian duct is sharply separated from a layer of cylindrical epithelium which is placed upon the middle and the lateral angles; this epithelium (*germinal epithelium*), which probably is derived from the epiblast, is the rudiment of the female generative apparatus, viz., in the middle, of the ova and the cells of the m. granulosa, and laterally of the epithelium which lines the Fallopian tubes and the uterus. The union of the median part with the connective tissue of the Wolffian bodies, which leads to the formation of the ovary, has already been spoken of. The lateral layer of epithelium is similarly surrounded by connective tissue and presents the appearance of a longitudinal cord, which later becomes hollow and gives rise to *Müller's duct*, which occupies the position of the future Fallopian tubes.

The two Müller's ducts open not far from the Wolffian ducts into the hindgut. Later on, their lower ends unite to form a common chamber, the uterus and vagina. Above, in the vicinity of the ovary, an opening forms in the ducts, and this opening is surrounded by fringes. The piece of the duct above the opening becomes reduced to the condition of a vesicle. In the male embryo the testicle arises from the genital part of the Wolffian

bodies; the canals of which becoming very much elongated and arranged in coils, are converted into the *tubuli seminiferi*, which penetrate the connective tissue of the testicle; that portion which has not penetrated forms the *epididymis*, and the ducts of the primordial kidneys form the *vas deferens*, with the *vesiculæ seminales*. The tubuli which do not form a part of the testicle are the *vasa aberrantia* of Haller. In the female the genital part of the Wolffian bodies remains as *Rosenmüller's organ*, or the *parovarium*, the efferent passage being converted into *the round ligament* of the uterus. In both sexes the renal part of the Wolffian bodies becomes reduced to the condition in which it is known as *the organ of Giraldes* or the *parepididymis*, and in the female as a separate structure situated close to the *parovarium*.

In the male, further, the seat of the ovary persists as a non-pedunculated cyst (Fleischl), whilst the ducts of Müller terminate below in the *uterus masculinus* (E. H. Weber) or *vesicula prostatica*, their upper end being represented by pedunculated cysts.

6. *The external urinary and sexual organs.* When with the closure of the navel, the urachus is shut off, the portion of the allantois which remains in the embryo forms the urinary bladder (the vertex of which remains connected with the navel by the urachus). The lowest part of the allantois, which contains the openings both of the urinary and the sexual organs, is called the *sinus urogenitalis*. On each side of the opening of the latter there arises two cutaneous projections, which in woman give rise to the *labia majora*, but which in man grow together above the opening, to form the scrotum, closing by a persistent seam which is called the *raphe*. In front of the opening, further, there arises an elongated body, which bears on its lower surface a furrow, which posteriorly runs into the *sinus urogenitalis*. The edges of this furrow unite in man to form the canal-shaped *urethra*, which opens at the apex of the elongated body, the penis; the posterior part of the urethra is formed by the urogenital sinus itself. In woman, however, the furrow remains open, and its edges grow into the *labia minora* or *nymphæ* whilst the original body itself forms the *clitoris*. The urogenital sinus becomes, however, so short that it merely forms a depression between the labia, into which the vagina and the

urinary bladder with a short urethra separately open. In the male embryo the descent of the testes takes place into the scrotum at the eighth month ; on this matter anatomical text-books are to be consulted.

Nothing is known in reference to the circumstances which influence the sex of the embryo. By statistics some have pretended to show that the relative ages of the parents have a certain influence in leading to a preponderance of males or females, still even this influence has been differently stated by different writers. Lately it has been asserted (Thury) that the sex depends upon the stage of maturity which the ovum has attained before impregnation ; according to this view ova are at first only capable of developing embyros of the female sex, and only after having undergone a change are they capable of producing males. But this is by no means generally proved.

7. The extremities originate as warty processes from the sides of the trunk, which only subsequently increase in length.

The development of the tissues, which is one of the most important sections in the history of development, is usually treated of as a part of Histology, and the reader is therefore referred, on this subject, to the works which specially treat of that branch of Anatomy.

The older theories of Pander, v. Baer, and Bischoff, assumed principally the existence of only two layers of the blastoderm—an external or 'animal,' corresponding to the somatopleure, and an internal ' vegetative,' corresponding to the splanchnopleure ; between these two that vascular system was supposed to originate from a separate vascular layer. A similar theory has lately been advanced by His, according to which, however, the whole system of connective tissues, the vessels, and the blood, are derived from the so-called ' white-yolk ' (of the bird's egg), which has quite a different origin from the 'principal yolk' (archiblast, neuroblast). It (i.e. the white yolk) originates in the cells of the m. granulosa which have migrated through the vitelline membrane into the principal yolk. The elements of the white yolk serve either for building up the embryo ('parablast,' 'hæmoblast') by migrating between the two layers of the blastoderm, or merely as ' food-yolk.' Another theory (Reichert's) accepts the process of splitting up of the mesoblast ('stratum intermedium.'), but differs from Remak's theory in not distinguishing a sensory (corneal) layer, and maintains that the original blastoderm persists as an enveloping membrane (' Umhüllungshaut '), whilst the proper layers are deposited within it afterwards. Between the enveloping membrane and the stratum intermedium originates the medullary plate as a special ' upper ' layer, limited to the germinal area. That portion of the enveloping membrane which becomes shut off in the amnion forms the epidermis of the skin of the embryo, and furnishes an epithelial covering to

the inner surface of the amnion ('endamnion'). Other recent modifications of the theory of Remak adopted in the text could not be here referred to without entering in a more special manner into the study of embryology.

The appended diagrammatic representations may serve to explain some of the fundamental points in development. With the exception of I., they are transverse sections of the embryo.
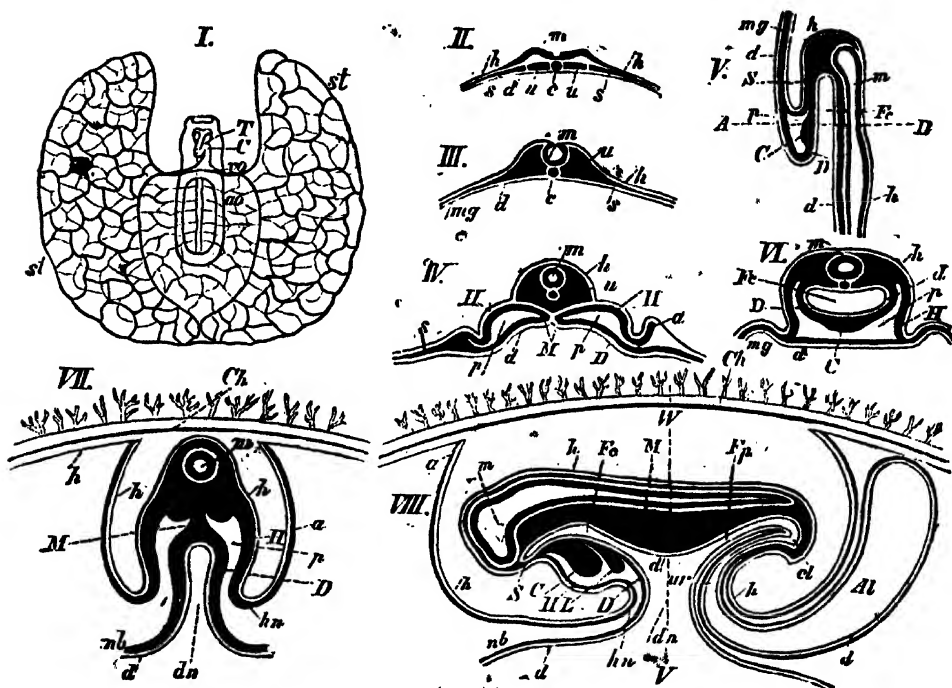
FIG. 42.

I. is a superficial view seen from the interior of the germ-vesicle; it shows the shoe-shaped embryo with the vessels of the area vasculosa. Across the anterior layer of the shoe, the already S-shaped heart is seen, from which superiorly there proceed two aortic roots, inferiorly, the two omphalo-meseraic veins. Through the opening of the shoe (the navel) the two still separated aortæ are seen, with the omphalo-meseraic arteries; in the area vasculosa the arteries are feebly, the veins strongly delineated.

The remaining figures are in part cross-sections (II., III., IV., VI., VII.), partly longitudinal sections of the embryo (V. and VIII.).

Section VI. corresponds to the line AB in the longitudinal section V.; the transverse section VII. corresponds similarly

to the line VW in VIII. The letters of reference are the same in all the drawings.

h	Epiblast	hn	Cutaneous navel
m	Medullary or neural tube	Fc	Fovea cardiaca (foregut)
mg	Mesoblast	Fp	Fovea posterior (hindgut)
d	Hypoblast	a	Amnion (peripheral part of the external part of the mesoblast detached and inverted; in Fig IV. on the left, it is yet connected with the internal part of the mesoblast; on the right it is detached).
e	Chorda dorsalis		
u	Protovertebral plates		
s	Lateral plates		
p	Pleuroperitoneal cavity		
H	External part of mesoblast		
D	Internal part of mesoblast		
M	Mesentery	Al	Allantois
S	Pharyngeal plate	ur	Urachus
Ch	Chorion frondosum	cl	Cloaca
nb	Umbilical vesicle	vo	Omphalo-meseraic veins
C	Heart	ao	Omphalo-meseraic arteries
T	Aortic arches	st	Sinus terminalis
dn	Omphalo-meseraic duct	L	Liver

So as to make the diagrams as intelligible as possible, in IV. and VII., the sections of the two aortæ and of the two Wolffian bodies are not shown.

Birth.

By the development of the ovum the uterus is more and more stretched, so that at the same time the cervix becomes obliterated. The uterine walls increase in thickness by the growth and by the new formation of its muscular fibres, as well as by the considerable development of its blood-vessels. At last, about 280 days after impregnation, by the operation of causes which are entirely unknown to us, the expulsion of the now developed ovum takes place. This expulsion is brought about by rhythmical and painful contractions of the muscular fibres of the uterus, which are technically known as 'pains,' and which are aided by the compression of the abdomen.

The following facts are known in reference to the innervation of the uterus :

Irritation of the hypogastric plexus gives rise to uterine contractions, and the same result is obtained by exciting the spinal cord up to the cerebellum ; the fibres which pass from the spinal cord to the uterus leave it in the vicinity of the last thoracic, and the third and fourth lumbar vertebræ. They pass along sympathetic paths, traverse the inferior mesenteric ganglion and run in one of the nerves which lie over the aorta, until they reach the uterus (Frankenhauser).

In addition to the nervous supply derived from the spinal cord, the uterus appears to possess nerve centres in its more immediate vicinity, perhaps scattered in part through its parenchyma. These centres are excited by the blood of dyspnœa (Oser and Schlesinger), like the centres in the medulla oblongata, and in the intestines, so that suffocation, compression of the aorta (Spiegelberg), hæmorrhage, &c. bring about uterine contractions. Even the centre presiding over uterine contractions, which is seated in the brain, is excited by the blood during dyspnœa, as well as by the circumstances previously mentioned (Oser and Schlesinger).

In the human being the ovum is not thrown off uninjured, but the embryo is first expelled, after the envelopes which surrounded it have been torn, and it is followed by the rest of the ovum. These envelopes are from without inwards—1. The *decidua reflexa* (p. 546). 2. The *chorion*, which, at the place where the allantois is situated (normally not at the orifice of exit of the uterus) forms the *placenta*, and which is free from villi over the *os uteri*. 3. The *amnion* (the umbilical vesicle forms an imperceptible structure in the placenta, compare p. 556).

As a result of the pressure of the first 'pains,' these membranes protrude in an arched form through the os uteri, and ultimately tear at one spot; after a large part of the *liquor amnii* has escaped, a part of the fœtus, usually the head, is set free. Now, with more or less rapidity, the process of expulsion sets in, hindered in part by the narrowness of the pelvis, in part by that of the os uteri, of the vagina and the vulva. Simultaneously, the placenta—not only its fœtal, but also its maternal part—taking with it a portion of the uterine mucous membrane—detaches itself from the contracting uterine wall, a process which is naturally accompanied by hæmorrhage. After the birth of the fœtus, the placenta, with the membranes which formed the walls of the ovum attached to its margins, though already detached, is still contained within the uterus, and the fœtus is united to it by means of the long umbilical cord. The latter contains the following structures:—1. The stalk of the allantois (a prolongation of the urachus), with the umbilical vessels, viz. the two arteries, which continue to pulsate, and the vein, which by the early intra-uterine rotations of the fœtus, is nearly always spirally twisted. 2. The shrivelled omphalo-meseraic duct with the umbilical vesicle. 3. Everything else which surrounds the tubular peduncle of the

amnion projecting from the navel, and which thus covers the inner side of the placenta, and passes over its margin to those of the chorion. The principal bulk of the umbilical cord is, however, formed by the three umbilical vessels, imbedded in a white connective tissue (*mucous tissue*), which is called 'Wharton's jelly.'

As soon as the detachment of the placenta commences, fœtal respiration through the intermediation of the maternal blood ceases, and in consequence of this a change in the gases of the blood commences, which leads to the *first respiration through the lungs* (Schwartz). The placenta which is contained in the uterus is no longer of service to the child, and the umbilical cord, of which the arteries cease to pulsate, can, after previous ligature of its fœtal end, be cut across, unless the expulsion of the placenta with the fœtal envelopes ('*after-birth*') be awaited. The skin of the newly-born child is covered with a sebaceous layer, which constitutes the *vernix caseosa.* After the expulsion of the afterbirth, and the arrest of the hæmorrhage by the continuing contractions of the uterus ('*after-pains*'), a regeneration of the uterine mucous membrane sets in, which is accompanied by a diminution of its muscular coat, and a new formation of muscular fibre cells; the first of these processes is associated with a mucous, and, at first, bloody discharge, which constitutes '*the lochia*.'

At birth the mammary glands of the mother begin to secrete (p. 121), and usually it is only on the cessation of the secretion, which takes place about ten months afterwards, that the process of menstruation, which had been arrested by impregnation, again becomes re-established.

D. DEVELOPMENT OF THE CHILD AFTER BIRTH.

At birth, neither the development of the structures nor of the functions of the young creature is arrested. The commencement of extra-uterine life, and the period which succeeds it up to *puberty*, are especially characterized by important processes of development. During this period (infancy and childhood) the development of the bones, and of the first and second teeth takes place, and growth is most energetic; above all, it is the period of the development of the mental powers, which from the

first low stages, when they approximate in their nature reflex actions, under the influence of the multiplicity of external influences, such as experience and education, develop ever more and more.

Growth is the term which is applied to express the increase in the dimensions of the body in all directions, as well as the increase of weight, due to the excess of the income of the body over its expenditure. The whole of the tissues and parts of the body take a part in this process, so that in general the *proportions* of the growing body are maintained. The most general conception of growth would treat it as being due to an *increase in the number* of tissue-forming elements, brought about in general as a result of cell-division, rather than as being due to an *increase in the size* of those which already exist, although this mode of growth also occurs.

The usual measure of its growth is the increase in the length of the body, and this is chiefly associated with the growth in length of the bones, which continues until about the twenty-second year. The growth in other dimensions, and the increase in weight, continues until about the fortieth year.

A diminution in *weight* occurs during the first days of life, and then again after from forty to fifty years of age; at the latter age this is associated with a diminution in the *length* of the body.

The life of man may be divided into the following periods: 1. 'Infancy,' which lasts from birth until the first dentition (the first 7 or 9 months); this is a period of most energetic growth, the length of the body increasing by two-thirds (20^{cm}).—2. 'Childhood,' which lasts until the second dentition (from 9 months until 7 years). The growth of the body in the second year amounts to about ten centimetres, in the third to about seven, and in each succeeding year about $5\frac{1}{2}^{cm}$.—3. Boyhood and Girlhood, which last until puberty (from 7 to 15 years).—4. Adolescence, which extends to the completion of the growth of the body (15 to 22 years).—5. Period of maturity (adult age), which lasts until 'involution' occurs in woman, and until retrograde changes occur in man, *i.e.* from the twenty-second until the forty-fifth year.—6. Age of gradual retrograde changes (old age), commencing about the forty-fifth year and lasting until death.

The retrograde changes which occur in the later periods of life consist in manifold processes of wear and contraction and destruction, in which that which is diseased is so little separated from that which is healthy as to preclude any detailed allusion to the phenomena in this place.

E. DEATH.

Death puts an end to those processes of the organism which are characteristic of 'Life,' and with death there sets in an assemblage of processes which are comprehended in the term Putrefaction.

There may be great difference of opinion as to which is the act which marks the close of life. Most naturally the *energies* of the body, its movements and its heat-production, especially the former, on account of their being easily recognised, appear to be conspicuous characteristics of life. It is obvious, how-ever, that amongst movements, only one which is automatic can serve as an index of life, and of such automatic movements the most regular as well as the most conspicuous are those of the heart. Usually then the *standing-still of the heart* is looked upon as a sign of death.

Although it may be urged that the cessation of a single function cannot be taken as a sign of the cessation of all others, yet a continued cessation of the movements of the heart is a *certain* sign of *approaching* death, as the function of every organ is associated with a supply of arterialised blood, and this cannot be afforded without the heart. The standing-still of the heart is, therefore, one of the most certain causes of death.

The inquiry into the *causes of death* leads to the following conclusions. As the activities of the body are the result of oxidation processes, there are three forms of general (somatic) death, which may be due to: 1. Deficiency in the material to be oxidized or of those inorganic matters which are indispensable to the vital processes, therefore, *defective nutrition.*—2. Deficiency in the *supply of oxygenized blood.*—3. An absence of the *conditions necessary to the oxidizing action* of oxygen.

Now as these circumstances can exert their action upon one or all of the parts of the body, there may be either a general or only a local death. The latter (*necrosis, gangrene*) may, in its turn, lead to general death, when it implicates an organ, the destruction of which is incompatible with life. The interlace-ment of the various processes of life renders it impossible to effect a strict separation between these three kinds of death; each of the three circumstances nearly always drags the others

after it; it is, therefore, only necessary to examine these individually in so far as they furnish the *primary* causes of death.

I. *Defective nutrition* constitutes a very frequent, though always a, remote, cause of death (cessation of the action of the heart or respiratory muscles being the proximate cause). According to its nature it leads to a gradual death. Death from hunger (p. 207), death which follows the inanition of old people, and also in part local death, due to local disturbances of the circulation, come under this category.

II. *The supply of arterialised blood* may be defective or cease altogether: 1. In consequence of the *absence of blood*, as when hæmorrhage occurs through the opening of large vessels or of the heart itself. If the hæmorrhage be not fatal, a restoration may be brought about by the action of water, yet the amount of the red blood corpuscles may be so small as to be insufficient to keep up the necessary exchanges of oxygen.—2. By *cessation of the circulation*: this occurs (*a*) locally, by closure of the arteries going to a part (as by ligature, thrombosis, embolism, or by their being cut), or by a hindrance to the flow of blood, due to obstacles in the veins; the consequence may be local, or it may even be general, death, if the disturbance of circulation affect the principal vascular trunks; (*b*) *generally, by a positive pressure in the thorax* (p. 67), or by *an arrest of the heart;* this may occur in consequence of injury or defective nutrition (atrophy) of the substance of the heart, of cessation of the circulation in the coronary arteries, of powerful irritation of the medulla oblongata, or of the vagi, or of defective supply of oxygen. A cessation of the circulation is conceivable in consequence of the cardiac movements being completely *ineffective, e.g.* by an injury to, or inefficiency of, the cardiac valves. 3. *By a hindrance to the absorption and retention of oxygen by the blood.* To this category belong all the influences mentioned at page 158, which lead to suffocation, of which some, viz. the cessation of the active movements of respiration, must now be examined more closely. The following circumstances lead to this: *a.* Paralysis of the respiratory centre in the medulla oblongata, due either to injury or destruction (*e.g.* by apoplexy); defective supply of blood or, of oxygen due to circumstances which have already been mentioned; lastly, the action of paralysing

poisons (such as chloroform). *b.* Impediments to the conducting power of nerves supplying the respiratory muscles, *e.g.* section or compression of the phrenic nerves and poisoning by curare. *c.* Paralysis of the respiratory muscles of the diaphragm. *d.* Tetanus of the respiratory muscles, as by strychnia-poisoning, or by irritation of the vagi. *e.* Mechanical hindrances to the expansion of the thorax, as pressure.—4. *By expulsion of the oxygen of the blood* (poisoning by carbonic oxide), or by a consumption of the oxygen of the blood (by means of reducing agents).

III. Very little is yet known concerning the circumstances required for the oxidation-processes of the body. It has already been mentioned (p. 231), that the mean temperature of the body is indispensable to life. Great or, at any rate, continuous rises and depressions of the temperature (heating or cooling with simultaneous abolition of the means of heat-regulation) lead to death. Possibly there are poisons which, like those which prevent putrefaction, render processes of oxidation impossible.

It belongs to the province of pathological science to investigate the modes in which diseases, injuries, and abnormal external circumstances, occasion death. Death from old age is usually designated as the physiological 'or natural' mode of death; this is a mode of death of which the proximate cause is unknown, but of which the remote causes are to be sought for in the diminished capacity for action of the organs of the body as a whole, and which is partly due to atrophy, partly to degeneration.

After the phenomena of 'rigor mortis' have passed away, the dead body falls a prey to putrefaction, unless this be prevented by very rapid desiccation or by the use of agents which oppose putrefaction. Putrefaction, concerning which little is yet known, consists in a slow oxidation of the organic constituents, brought about by the oxygen of the air, under the influence of a ferment, such as vibrios must probably be considered (Pasteur).

The marks of post-mortem lividity (suggilations, livores) are precursors of putrefaction, which, in addition to cadaveric rigidity, afford an almost certain proof of death; these marks are occasioned by the blood-colouring matter diffusing out of the blood-corpuscles, first into the serum, and afterwards into the fluids moistening the arterial walls, the parenchyma of organs and the skin.

ADDENDUM.

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Appendix to the Mechanism of Respiration (p. 170).

THE introductory passages concerned in respiration are the nasal apertures, the pharyngo-nasal cavity, the larynx, and the trachea. Respiration by the mouth, although frequently voluntary, as a rule merely serves to replace that by the nose, when the passages of the latter are from any cause obstructed. The above-mentioned channels in part subserve the purposes of respiration by means of suitable arrangements with which they are provided, and in part are the seat of certain movements which are induced in them by the motions of respiration. The inspired air, in passing along them to the lungs, is warmed, and deprived, by contact with the walls, of the coarser solid impurities which it may contain. These particles, as well as superfluous mucus, &c., are driven outwards by the waving cilia which are present on nearly every portion of the walls.

The larynx further possesses in the vocal cords an apparatus for preventing the entrance into the trachea of foreign bodies, such as saliva, small portions of food, &c., as well as of certain irritating gases; for every stimulus causes reflex closure of the glottis. If the glottidean muscles be paralysed by section of the vagi, or of the inferior laryngeal branches of the vagi, such foreign bodies gain entrance into the lungs easily, and induce fatal inflammations (Traube).

The expulsion of foreign particles which have either found their way into the respiratory passages, or have arisen there as pathological products (mucus), is brought about by the stimulation of the mucous membrane which they cause, and which induces, in a reflex manner, an explosive expiratory blast of air, by which they are driven out. Such explosive expiration is called *sneezing* when the nasal cavities are concerned, and *coughing* when the irritant is in the larynx. Each is accompanied by a noise produced by the sudden bursting open of a closed aperture, which in sneezing is formed by the apposition of the velum palati to the pharyngeal wall, and in coughing by the apposed vocal cords. Coughing may be induced by mechanical irritation of any portion of the respiratory mucous membrane from the lower surface of the upper vocal cords to the alveoli, but it is especially violent when the irritant is applied at the larynx, or at the place of bifurcation of the trachea below (Nothnagel). The sensory nerves im-

plicated in the reflex act of sneezing are the trigeminal nerve, and possibly also the olfactory nerve, and in coughing probably the superior laryngeal branches of the vagi especially. Coughing may also be voluntary. It is quite possible that the bronchial muscles referred to previously (p. 161) may assist in expelling mucus, &c. from the finer bronchial tubes.

Expired air may be used *voluntarily* for purposes similar to those just discussed. For example, mucus may be driven from the nose, the nostrils being voluntarily compressed from without in the process of what is called 'blowing the nose;' or through the isthmus of the fauces, which is narrowed by muscular action, as in 'clearing the throat.' Fluids which it is desired to keep in the throat for some time without swallowing are prevented from entering into the air-passages by keeping up a stream of expired air, which, as it escapes through the fluid in bubbles, causes the characteristic noise of 'gargling.' Warm and moist air expired through the widely-opened mouth may be used for the purposes of heating and moistening. Finally, vocal cords, uvula, tongue, lips, or any of the other apparatuses of the mouth for the purpose of vocalising, may be set in sonorous vibration, as in 'singing,' 'speaking,' 'blowing.' (Voice and speech are discussed in Chapter VIII.)

If the glottis be closed after a deep inspiration, and the abdominal muscles then powerfully contracted, the viscera of the abdomen become strongly compressed, and such pressure may aid in the expulsion of the contents of the various abdominal organs—rectum, uterus, and bladder (abdominal pressure).

NOTES

BY THE AUTHOR.

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PAGE 36.

According to more recent researches (Hoppe-Seyler and Diaconow), protagon must be regarded as a combination in which lecithin is contained in addition to cerebrin. Cerebrin (W. Müller), $C_{17}H_{33}NO_3$ (?), is a glucoside, and exhibits the property, ascribed to protagon, of swelling up on the addition of water. When decomposed by means of mineral acids it yields, in addition to other, as yet uninvestigated, products, a body of the sugar-group which deflects the plane of polarisation to the left.

PAGE 73.

The hypothesis given in the text, in consequence especially of researches on certain poisons, now appears to have become as untenable as the older view, according to which there exist in the heart, and particularly in the auricles, inhibitory centres in connection with the vagus, but possessing a tonus of their own. There are certain poisons, of which muscarine is the chief, which induce, even after section of the vagi, a stand-still of the heart in diastole, during which condition every stimulus is followed by a single contraction. Atropia, on the contrary, causes the heart to beat more quickly, and interferes in the results of vagus-irritation and in the action of muscarine. It is not sufficient to explain these effects as due to irritation or paralysis of the inhibitory vagus-endings; for nicotine (which operates like atropia, except at the onset, when its action seems to be the reverse) does not prevent the stand-still due to muscarine, and therefore paralyses portions of the nerve nearer to the centre than those acted on by atropia. The portions of the nerve in the latter case are probably the vagus-ending, while muscarine and atropia act upon the ganglionic inhibitory apparatus (Schmiedeberg, Böhm).

Hence Stannius's experiment would have to be explained by assuming that, after the separation of the sinus-ganglion, the inhibitory centres in the whole separated portion (auricles and ventricles) overcome the motor centra, while in the ventricle by itself the latter kind only are present (von Bezold).

That the vagus contains accelerating as well as inhibitory fibres is established by this fact, among others, that in poisoning by atropia irritation of the vagus causes the heart to beat *more quickly* (Schmiedeberg).

PAGE 111.

According to later researches (Heidenhain), easily recognisable substances which pass into the urine, such as sulph-indigotate of sodium, do not appear in the capsules and in the straight uriniferous tubules, but only in the convoluted tubules, after they have been injected into the blood-vessels. This shows that the capsules effect the separation of water alone, and perhaps also of salts, the specific constituents of the urine being secreted from the blood by the epithelium of the convoluted tubules. This circumstance supports the theory of Bowman against that of Ludwig concerning the secretion of urine, as does also the observation of von Wittich, referred to in the text, respecting the kidneys of birds, which observation may be confirmed in the case of mammalia after the injection of sodium urate. Additional importance must be attached to these facts, since, after the functions of the capsule have been abolished by cauterising the cortex, the tubuli still take up colouring matter, which, however, on account of the deficient supply of water, remain in them (Heidenhain).

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